ABSTRACT OF PH.D. THESIS

The wing-venation of the Orthoptera Saltatoria. D.R. Ragge.

1. Comstock and Needham in their work on the homologies of insect wing-veins barely mentioned the wings of the Saltatoria, though briefly describing the tracheation of a few nymphal wing-pads. The author's intention has been to fill in the resulting gap in insect morphology, and thus to facilitate studies on the phylogeny and systematics of the Orthoptera.

2. Over 600 Saltatorian genera were examined. These included representatives of all the winged families and of almost all the winged subfamilies. The wings of over 60 representative species are figured.

3. The criteria used in elucidating the homologies of the veins were those of tracheation, form, position, convexity and concavity, basal articulation and macrotrichia. Palaeolontological evidence was also studied.

4. From a consideration of these criteria, names based on the Comstock-Needham System are given to the wing-veins and wing-areas of all the winged Saltatorian families. In the case of the Tridactylidae the conclusions are only tentative as no nymphs were available for tracheation studies.

5. A brief account of Dictyopteran wing-venation is also given, the tracheation of representative wing-pads of the Mantoidea being examined apparently for the first time.

6. The wing morphology of the Saltatoria throws much light on the phylogeny of the group. The Acridoidea have clearly been quite independent of the remaining Saltatoria in their evolutionary history and have probably had no direct connection with the Protorthoptera. The author suggests that the wing-venation of the Pneumoridae (which is more primitive than that of any other Acridoid family) has been derived with little modification from Palaeodictyoptera of the *Stenodictya* type.

7. The author demonstrates that the anterior media (*sensu* Lameere) - probably absent in most insects - is almost certainly present in the Saltatoria.

8. A hypothetical 'standard fossil wing' is constructed which satisfies all the requirements of the wings of a Saltatorian ancestor.

THE WING-VENATION OF THE ORTHOPTERA SALTATORIA (INCLUDING SPECIALIZATION FOR STRIDULATION).

D. R. RAGGE

Entomology Department,
British Museum (Natural History),
London, S.W.7.

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I. INTRODUCTION

1. GENERAL

Although the taxonomic value of the wings in many groups of Saltatoria has been widely recognized, practically no work has been done on the homologies of the veins. The attempts which have been made to apply names based on the Comstock-Needham System to the veins are of a very conflicting nature: no two authors are in complete agreement on the subject. As most of the studies have been confined to single families (or even species) there has been little uniformity throughout the group, and a formidable array of synonyms has arisen in connection with the nomenclatures proposed. The aim of the present work is to determine, on the basis of all the possible criteria, the homologies of Saltatorian wing-veins, and thus to apply to them a uniform and unmodified Comstock-Needham terminology. This, it is hoped, will fill in a large gap in insect morphology, and facilitate studies on the phylogeny and systematics of the Orthoptera.

Much of the past disagreement about Saltatorian wing-venation has arisen through the neglect of some of the most useful criteria for naming the veins. Comstock and Needham (1899) published diagrams of the tracheae in Acridid, Tettigoniid,

and Gryllid wing-pads, but made no attempt to name the adult veins. Since this work the tracheation of the nymphal wing-pads has been largely ignored. In 1902 Hancock published diagrams of adult Tetrigid wings in which the bases of some of the tracheal stems could be seen. Karny (1925) studied the tracheation of Gryllacridid wing-pads; in this case the treatment was detailed and the interpretation accurate. Vignon (1929) gives excellent figures of the tracheation of some Tettigoniid nymphs, but applies a new nomenclature to them. In 1933 Forbes published a diagram of the tracheation of the wing-pads of Scapteriscus didactylus (Latreille). Hsüeh (1938) has published an account of the tracheation and venation of the Tettigoniid Gampsocleis gratiosa Brunetti; it is unfortunate that this careful study was carried out on a brachypterous species. In 1939 Zeuner, in his work on the fossil Ensifera, gave diagrams of the tracheation of the fore wing-pads of Tettigonia, Decticus, and Brachytrypes, but his terminological conclusions were based on fossil evidence rather than tracheation studies. The only other work on Saltatorian tracheation is that of Karandikar (1945), who describes the development of the wing-pads of Schistocerca gregaria (Forskal) but barely mentions the adult venation.

Among the Dictyoptera, Blattoid tracheation (and venation) has been fully dealt with by Comstock and Needham (1899) and subsequent authors (of which the most recent is

Smart, 1951), but the Mantoidea have apparently been completely ignored in this respect.

Phasmid tracheation is known only by one published work, that of Burt (1932) on Pulchriphyllium crurifolium (Serville).

Zeuner (1939) has discussed in fair detail the evidence afforded by the fossil wings of the Tettigonioidea, Grylloidea, and, to a rather less extent, Acridoidea. As will be seen later, however, a re-examination of most of the fossils concerned has made it clear that conclusions based on this criterion alone must be very tentative.

Among the other criteria available, those of position and form are in general use; basal articulation has been studied in the Acrididae and Tettigoniidae (Snodgrass, 1929; La Greca, 1947; Ivanova, 1947); convexity and concavity have been almost universally ignored (but see Vignon, 1929); and macrotrichia, which are, however, only of limited use in the Acridoidea, have received no mention in this respect.

A brief history of the relevant literature and a table of synonymy is given for each group from Section VII onwards.

2. TREATMENT ADOPTED IN THIS WORK

It has been thought best to have the actual descriptions of venation unencumbered by lengthy accounts of the reasons for the application of each name, and all explanatory matter of this nature is given beforehand in Section VI. The wing-venation

and nymphal tracheation are described in each family separately (except in the case of the Acrididae and Eumastacidae which have a very similar venation and are treated together); the last section under each superfamily is a comparative discussion, comparing and contrasting the venation of each component family. Sections XXII and XXIII are respectively a brief resumé of the features of Blattoid wings and an introductory account of those of the Mantoidea. A concluding Section gives a general comparison between the superfamilies, and between the Saltatoria, Dictyoptera, and other orders, together with a discussion on the contribution of the wing morphology to the phylogeny and systematics of the Orthoptera.

Throughout the work, authorities for generic and specific names are given only where these names are first mentioned.

II. CLASSIFICATION

The classification of the major groups of Orthoptera (s. lat.) has always been a matter of some difficulty. A large and diverse assemblage of rather generalized insects has been grouped together in this order, on the basis of such features as the sclerotized fore wings, fan-like hind wings, shield-like pronotum, and typical biting mouthparts. These insects fall into two principal groups: the Cursoria with normal hind femora and five-segmented tarsi, and the Saltatoria with swollen hind femora and tarsi with less than five segments. Originally, the Grylloblattidae and Phasmida were looked upon as Cursorial insects, but as the anatomy of these insects has become better known it has become evident that these two groups are no more related to the Cursoria than to the Saltatoria. In recent years, in fact, it has become customary to separate the Blattidae (s. lat.) and Mantidae (s. lat.) as a distinct order, the Dictyoptera, leaving the remaining groups as the Orthoptera (s. str.). This arrangement, however, has the disadvantage that the Orthoptera (s. str.) cannot be satisfactorily defined. In this work, therefore, the Orthoptera (s. lat.) is regarded as containing four groups of ordinal value: Grylloblattodea, Saltatoria, Phasmida, and Dictyoptera. This division is anatomically clear-cut and leads to no difficulties of definition; there is little doubt that the four groups have been phylogenetically distinct since Carboniferous times.

The classification used in this work is set out below.

Order GRYLLOBLATTODEA

GRYLLOBLATTIDAE

Order SALTATORIA

Superfamily ACRIDOIDEA

PNEUMORIDAE

LOCUSTOPSIDAE (extinct)

ACRIDIDAE
- Catantopinae
- Paulininae
- Pamphaginae
- Pyrgomorphinae
- Ommexechinae
- Trigonopteryginae
- Charilainae
- Oedipodinae
- Acridinae

EUMASTACIDAE
- Morabinae (apterous)
- Tanaeocerotinae (apterous)
- Teicophryinae (apterous)
- Gomphomastinae (apterous)
- Morseinae (apterous)
- Mastacideinae (microalate)
- Eumastacinae
- Biroellinae (apterous or brachypterous)
- Eruciinae
- Chorotypinae
- Chininae
- Espagnolinae
- Episactinae (apterous)
- Malagassinae (apterous)
- Miraculinae (apterous)
- Thericleinae (apterous or brachypterous)
- Euschmidtiinae

PROSCOPIIDAE (apterous or microalate)

TETRIGIDAE

Superfamily TRIDACTYLOIDEA

TRIDACTYLIDAE
- Tridactylinae
- Rhipipteryginae

CYLINDRACHETIDAE (apterous)

Superfamily TETTIGONIOIDEA

RAPHIDOPHORIDAE (apterous)

PROPHALANGOPSIDAE
- Haglinae (extinct)
- Prophalangopsinae
- Cyrtophyllitinae (extinct)
- Geinitziinae (extinct)

GRYLLACRIDIDAE
- Palaeorehniinae (extinct)
- Stenopelmatinae
- Lezininae
- Gryllacrinae
- Henicinae
- Deinacridinae

ELCANIDAE (extinct)

TETTIGONIIDAE
- Termitidiinae (extinct)
- Rammeinae (extinct)
- Ephippigerinae (brachypterous)
- Pycnogastrinae (brachypterous)
- Bradyporinae (brachypterous)
- Deracanthinae (brachypterous)
- Hetrodinae (brachypterous)
- Acridoxeninae
- Pterophyllinae
- Pseudophyllinae
- Meconeminae
- Mecopodinae
- Phyllophorinae
- Tettigoniinae
- Decticinae
- Saginae
- Salomoninae
- Agraeciinae
- Copiphorinae
- Conocephalinae
- Listroscelinae
- Tympanophorinae
- Phaneropterinae

Prochilinae
Simoderinae
Aspidonotinae
Moristinae

SCHIZODACTYLIDAE

Superfamily GRYLLOIDEA

GRYLLIDAE
Protogryllinae (extinct)
Gryllinae
Eneopterinae
Oecanthinae
Trigonidiinae
Mogoplistinae
Myrmecophilinae (apterous)

GRYLLOTALPIDAE
Gryllotalpinae
Scapteriscinae

Order PHASMIDA

Order DICTYOPTERA

Superfamily BLATTOIDEA

Superfamily MANTOIDEA

III. MATERIAL

Altogether, about 630 Saltatorian genera were examined. A list is given below of only those genera which have been mentioned in the text or illustrated. The number of genera examined in each family is given, and a complete list will be found in the Appendix.

Where a particular species is used, the specific name (when known) is given in the text. Where only the generic name is given in the text, the remarks generally apply to all the fully-winged species of the genus. Many of the figured wings were from insects whose specific names were uncertain, but they may always be taken as typical of the macroalate members of the genus. The genera which have representative wings figured are marked below thus (^{x}); those which have the tracheation of the wing-pads of representative nymphs illustrated are marked thus (^{n}).

PNEUMORIDAE (5 genera examined)

Bulla Linnaeus

Pneumora Thunberg

Cystocoelia Audinet-Serville

Shortridgea Péringuey^{x}

Prostalia Bolivar

LOCUSTOPSIDAE (4 genera examined)

Locustopsis Handlirsch (fossil)[x]

ACRIDIDAE (360 genera examined)

Romalea Audinet-Serville (Catantopinae)[x]

Choroedocus Bolivar (Catantopinae)[x]

Euprepocnemis Stal (Catantopinae)

Teratodes Brullé (Catantopinae)[xn]

Paulinia Blanchard (Paulininae)[x]

Lamarckiana Kirby (Pamphaginae)[x]

Aphantotropis Uvarov (Pamphaginae)

Poecilocerus Stal (Pyrgomorphinae)[x]

Phymateus Thunberg (Pyrgomorphinae)

Parossa Bruner (Ommexechinae)[x]

Systella Westwood (Trigonopteryginae)[x]

Trigonopteryx Charpentier (Trigonopteryginae)

Charilaus Stal (Charilainae)

Locusta Linnaeus (Oedipodinae)[x]

Psophus Fieber (Oedipodinae)[x]

Dissosteira Scudder (Oedipodinae)[x]

Myrmeleotettix Bolivar (Acridinae)[x]

Chorthippus Fieber (Acridinae)[x]

Acrida Linnaeus (Acridinae)[x]

Omocestus Bolivar (Acridinae)[x]

Mecostethus Fieber (Acridinae)[x]

EUMASTACIDAE (6 genera examined)

Chorotypus Serville (Chorotypinae)[x]

Erianthus Stal (Chorotypinae)[x]

Euschmidtia Karsch (Euschmidtiinae)[x]

TETRIGIDAE (8 genera examined)

Eugavialidium Hancock[x]

TRIDACTYLIDAE (2 genera examined)

Tridactylus Olivier (Tridactylinae)[x]

Rhipipteryx Audinet-Serville (Rhipipteryginae)[x]

PROPHALANGOPSIDAE (5 genera examined)

Hagla Giebel (Haglinae) (fossil)[x]

Prophalangopsis Martynov (Prophalangopsinae)[x]

Cyphoderris Uhler (Prophalangopsinae)[x]

Pamphagopsis Martynov (Prophalangopsidae) (fossil)

Zalmona Giebel (Prophalangopsinae) (fossil)

GRYLLACRIDIDAE (7 genera examined)

Palaeorehnia Cockerell (Palaeorehniinae) (fossil)

Jurassobatea Zeuner (Palaeorehniinae) (fossil)

Macrelcana Karny (Stenopelmatinae) (fossil)

Gryllacris Audinet-Serville (Gryllacrinae)[x]

ELCANIDAE (1 genus examined)

Elcana Giebel[x]

TETTIGONIIDAE (211 genera examined)

Termitidium Goldenberg (Termitidiinae) (fossil)

Pycnogaster Graells (Pycnogastrinae)[x]

Bradyporus Charpentier (Bradyporinae)[x]

Acridoxena White (Acridoxeninae)[x]

Cycloptera Audinet-Serville (Pterophyllinae)[x]

Thliboscelus Audinet-Serville (Pterophyllinae)[x]

Diophanes Stal (Pterophyllinae)

Morsimus Stal (Pseudophyllinae)

Xerophylloptexyx Rehn (Pseudophyllinae)[x]

Sathrophyllia Stal (Pseudophyllinae)[x]

Mioacris Pictet & Saussure (Pseudophyllinae)

Tympanoptera Pictet & Saussure (Pseudophyllinae)

Climacoptera Redtenbacher (Pseudophyllinae)

Meconema Audinet-Serville (Meconeminae)[x]

Mecopoda Audinet-Serville (Mecopodinae)[x]

Corycus Saussure (Mecopodinae)

Pachysmopoda Karsch (Mecopodinae)

Phyllophora Thunberg (Phyllophorinae)[x]

Phyllophorella Karny (Phyllophorinae)[x]

Tettigonia Linnaeus (Tettigoniinae)[xn]

Decticus Audinet-Serville (Decticinae)[xn]

Chlorobalius Tepper (Decticinae)

Platycleis Fieber (Decticinae)[x]

Clonia Stal (Saginae)[x]

Salomona Blanchard (Salomoninae)

Macroxiphus Pictet (Salomoninae)

Homorocoryphus Karny (Copiphorinae)[x]

Copiphora Audinet-Serville (Copiphorinae)

Hexacentrus Audinet-Serville (Listroscelinae)[x]

Lesina Walker (Listroscelinae)[x]

Tympanophora White (Tympanophorinae)[x]

Phaneroptera Audinet-Serville (Phaneropterinae)[x]

Tetraconcha Karsch (Phaneropterinae)

Prochilus Brullé (Prochilinae)[x]

Simodera Karsch (Simoderinae)

Narea Walker (Moristinae)

SCHIZODACTYLIDAE (1 genus examined)

Schizodactylus Brullé[x]

GRYLLIDAE (14 genera examined)

Protogryllus Handlirsch (Protogryllinae) (fossil)

Mesogryllus Handlirsch (Protogryllinae) (fossil)[x]

Acheta Fabricius (Gryllinae)[xn]

Brachytrypes Agassiz (Gryllinae)

Gryllodes Saussure (Gryllinae)

Nemobius Audinet-Serville (Gryllinae)

Paranemobius Saussure (Gryllinae)

Eneoptera Burmeister (Eneopterinae)[x]

Euscyrtus Guérin-Méneville (Eneopterinae)

Oecanthus Audinet-Serville (Oecanthinae)[x]

Phaeophilacris Walker (Oecanthinae)

Paragryllus Guérin-Ménéville (Oecanthinae)

Homeogryllus Chopard (Oecanthinae)

Trigonidium Audinet-Serville (Trigonidiinae)[x]

GRYLLOTALPIDAE (2 genera examined)

Gryllotalpa Latreille (Gryllotalpinae)[xn]

Scapteriscus Scudder (Scapteriscinae)[x]

MANTOIDEA (5 genera examined)

Ameles Burmeister[xn]

Sphodromantis Stal[xn]

Bolbena Giglio-Tos

Rivetina Berland & Chopard

Empusa Huebner[x]

IV. TECHNIQUE

1. PREPARATIONS OF WING-PAD TRACHEATION

These preparations were made in three ways:-

(a) Temporary preparations using glycerine jelly.

The fresh nymphs were immersed in pure glycerine. After about six hours the wing-pads were carefully removed under glycerine, together with the pleura of their respective segments (this ensured that the basal parts of the tracheation remained intact). The wing-pads were then conveyed to a small quantity of melted glycerine jelly on a slide; a cover slip was lowered on carefully, and the jelly cooled as rapidly as possible. The tracheation was drawn as soon as the jelly had set. Using a firm jelly, these preparations last up to two weeks.

By this method the tracheae are rendered visible in transmitted light by virtue of the air inside them, which has a very different refractive index from glycerine jelly, and the technique is designed to prevent the air being replaced by liquid. When last stage nymphs are used, it is generally necessary for them to be in the early part of the instar, as the developing wing later obscures the tracheation. In forms with heavily pigmented wing-pads, it is often essential to use recently moulted nymphs.

(b) Permanent preparations using an injection technique.

This method was developed by Wigglesworth (1950) and is adequately described by this author. The tracheae are rendered opaque by being filled with cobalt sulphide, and are thus visible in silhouette using transmitted light.

(c) Permanent preparations using a high refractive index medium.

Insect tracheae are supported by chitinous taenidia which are practically invisible when mounted in Canada balsam. If, however, a nymphal wing-pad is mounted in a medium with a sufficiently high refractive index (such as 'Naphthrax', refractive index, when dry, 1·76-1·80, prepared in xylol by G.T. Gurr), the tracheae become clearly visible. This method can be used with preserved material and is often successful with dried specimens; it is advisable, however, to use nymphs which have recently moulted.

2. PREPARATIONS OF ADULT WINGS

For drawing purposes the wings were generally mounted in air between two glass slides held together with rubber bands. The hind-wings were first moistened to facilitate spreading them out.

For microscopical examination preparations in 'Euparal' or 'Naphthrax' were used. With the latter medium it was frequently possible to see the tracheation of the adult wings,

thus obviating the use of nymphs; this was true of both preserved and dry material, and was particularly useful in the Pneumoridae.

Attempts to inject the tracheae of the wings of newly-emerged adults were only partially successful, some tracheae offering more resistance than others.

3. DRAWINGS

The drawings of adult venation were almost always made with a photographic enlarger. The wings (in an air preparation) were placed on the negative stage, and the image (at a suitable enlargment) was traced on to Bristol board below. Wings or parts of wings which were too small for the enlarger were sometimes drawn with the aid of a camera lucida; this method, however, almost inevitably produces slight distortion, and was therefore avoided whenever possible. Drawings in which reflected light was necessary and in which distortion was particularly undesirable (e.g. those of the axillary sclerites) were made using a 'squared' eyepiece.

The reproductions of published drawings were drawn using the projected image from an epidiascope.

V. GENERAL ACCOUNT OF ORTHOPTEROID WING-VENATION

As there has been little work in the past on the wing-venation of the Orthoptera, it is proposed to give here an introductory account of the characteristics of the wings of these insects, so that the more detailed matter to follow may be better understood.

Perhaps the most distinctive feature of Orthopteroid wings is the expanded area of the hind wing, often referred to as the 'anal' fan. This is found throughout the Saltatoria and Dictyoptera, reaching perhaps its most advanced form in the Tridactyloidea. The wing-areas incorporated in the 'anal' fan vary in the different groups. In the Acridoidea, Tridactyloidea, and Dictyoptera, it is only the anal area which is concerned, and the term anal fan is thus appropriate. In Tettigoniid wings, however, the cubital area is also included and the term cubito-anal fan is preferable. In the Grylloidea (and Schizodactylidae) the folding of the hind wing extends over the whole of its area.

The venation of Saltatorian fore wings is characterized by the distinctive costa, which generally lies well behind the anterior margin. This feature is rather obscured in the Grylloidea, as the costa is very reduced or absent. The anterior margin of the fore wing is either unsupported or strengthened with an ambient vein. Ambient veins are common

in the Acridoidea (though not in the Tetrigidae), Tettigoniidae, and Schizodactylidae, but are not generally found in the other Tettigonioid families or in most Grylloid wings.

In some respects Orthopteroid wings are very primitive. For example, there is commonly a small amount of archedictyon, especially at the base of the wing, and the anterior media (in the Lameerian sense - Lameere, 1922) is almost certainly present in most cases. The radial sector exhibits the pectinate form of branching which is common in the earliest insect fossils. In some of the families, much of the primitive corrugation of the wings has been retained. This is especially true of the Pneumoridae and the fossil family Elcanidae. The costa, subcosta, radius, and first anal, still exhibit their primitive convexity and concavity in many of the other families.

The cubitus of the Saltatoria and Dictyoptera is distinctive in having its bifurcation into Cu_1 and Cu_2 more proximal than usual, generally right at the base of the wing. In the Saltatoria, Cu_2 shows an almost universal tendency to be reduced or poorly developed (especially in the hind wing), though an important exception to this is found in the male fore wings of the Tettigoniidae and Grylloidea, in which Cu_2 forms the stridulatory rib. The Orthopteroid Cu_2 is almost invariably a single stem, whereas Cu_1 is frequently branched.

Accessory veins and intercalary veins are common in the wings of Orthoptera, but groups are found in which either the one or the other type, or both types, are absent. Accessory

veins are particularly abundant in the fore wings of the Tettigoniidae and Grylloidea.

The fore wings are almost invariably arranged so as to cover the more delicate hind wings when at rest, and they frequently have a leathery texture to facilitate this protective function. In the Tridactyloidea and Tetrigidae, the fore wings are heavily sclerotized and have a very reduced venation.

Orthopteroid fore wings are commonly modified for leaf-mimicry. This is especially true of the Tettigoniidae, in which a very large proportion of the species are leaf-mimics. In these forms, the fore wings are green, but a wide variety of colours is exhibited by the other families. Though the hind wings are usually colourless and transparent, forms with coloured hind wings are not uncommon, and the pigmentation is sometimes sufficient to render the membrane opaque.

The use of the wings for stridulation is a widespread character of the Saltatoria. In the Acrididae, there are two principal mechanisms: in some forms the medial intercalary vein of the fore wing is toothed, and the hind femur ridged; in others the hind femur bears stridulatory pegs - in both these cases the sound is produced by the hind femora being rubbed against the flexed fore wings. In the Tettigoniidae, stridulation is entirely alary and is effected by rubbing the tooth-bearing Cu_2 of the left fore wing against the hind margin of the right fore wing. The left fore wing thus always overlaps the right one. In the Grylloidea, the process is similar

but the right fore wing overlaps the left one. The constant nature of the arrangement of the flexed fore wings has resulted in asymmetry in the males (and a few females) of the Tettigoniidae, but in the Grylloidea the male fore wings are practically identical, and a reversal of their positions (though rarely occurring in practice) would not affect stridulation.

When the wings are used for stridulation, the membrane is frequently modified to act as a resonator. This has resulted in the 'harp' and 'mirror' of the Gryllidae, and the 'mirror' of the Tettigoniidae. In the Acrididae the effect is not so pronounced, but in some forms some of the areas of the male fore wing are greatly expanded for this purpose.

VI. REASONS FOR THE APPLICATION OF THE HOMOLOGIES PROPOSED IN THIS WORK

In order to render the descriptions of venation less cumbersome, the reasons for the application of the names used are given separately in this Section. The criteria which have been of use are listed below:-

(a) evidence from fossil forms

(b) evidence from present-day forms

(i) tracheation

(ii) form

(iii) position

(iv) convexity and concavity

(v) basal articulation

(vi) macrotrichia

Each superfamily is dealt with in a separate account, and a brief résumé of the important criteria used in ~~naming~~ identifying each vein is given at the end of each of these accounts. (The Tridactyloidea and Dictyoptera are not included here for reasons which will be made clear by reading the introductory remarks to these two groups in Sections XII and XXII.) Introductory matter concerning each criterion, and additional remarks on the importance of 'mutual confirmation', are given in the first account, that of the Acridoidea; it should be noted that these remarks also apply to the other groups.

It is unavoidable that the descriptive accounts following this Section will be frequently anticipated in it; when there is any doubt as to which vein is indicated by any particular name, it is assumed that reference will be made to these descriptions.

1. THE ACRIDOIDEA

(a) Evidence from fossil forms.

Fossil Acridoidea are conspicuously scanty. The fossil Acrididae are practically identical with present-day forms. The extinct Locustopsidae show only one major difference from the Acrididae in their wing-venation: the three-branched media. As a media branching in the same way is found in no other Acridoidea (except as a chance variation), and in no fossils likely to be ancestral to this group, it seems probable that the three-branched media has been secondarily acquired by the Locustopsidae (i.e. acquired after this family had separated from any evolutionary lines ancestral to other Acridoidea).

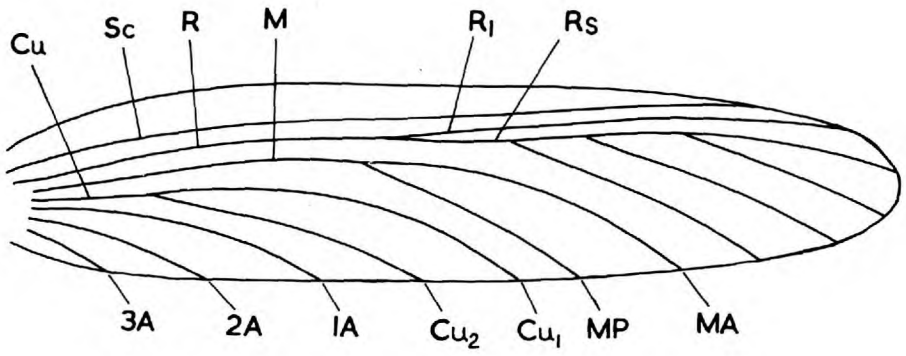
It is only among the Palaeodictyoptera (e.g. Dictyoneuridae Handlirsch, and Pteronidiidae Bolton) that there are fossils with a wing-venation resembling the most primitive Acridoid venation (that of the Pneumoridae). In particular, Stenodictya lobata Brongniart (Dictyoneuridae) has a venation closely resembling that of the Pneumoridae (especially Bulla).

This correspondence is most striking in the fore wing, where the only differences between Stenodictya Brongniart and Bulla are the submarginal costa, the closer approximation of Sc, R, and M, the more proximal bifurcation of Cu, and the loss of some of the primitive convexities and concavities, in the latter genus. The following features of the fore wing are common to the two genera and are found combined nowhere outside the Palaeodictyoptera and Acridoidea:-

1. The archedictyon covering the whole wing, and hence the absence of cross-veins and intercalaries.
2. The pectinate radial sector.
3. The simply bifurcate M and Cu.
4. The primitive corrugation of Sc, R, and M.

The resemblance can be appreciated more easily by reference to Fig. 1. The hind wings of the Pneumoridae show additional specializations (the basal fusion of R and M, and the development of the anal lobe).

It is not improbable, then, that the Pneumoridae and later Palaeodictyoptera are in some way connected phylogenetically, and this provides some slight confirmation of the homologies given to Pneumorid wing-veins on the basis of other criteria, particularly tracheation and form (there can be no doubt that the nomenclature applied to the wings of Stenodictya in Fig. 1 is correct, as the veins are primary by definition- see p. 67 - and their identity is simply established from their position- see p. 39 - and confirmed by their mode of branching -



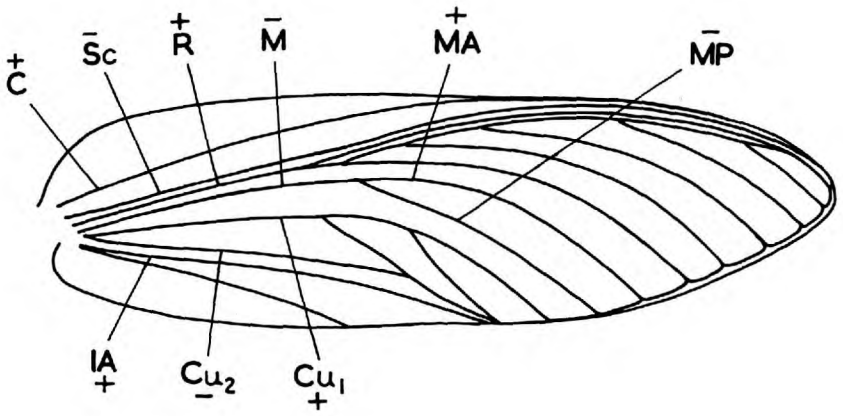


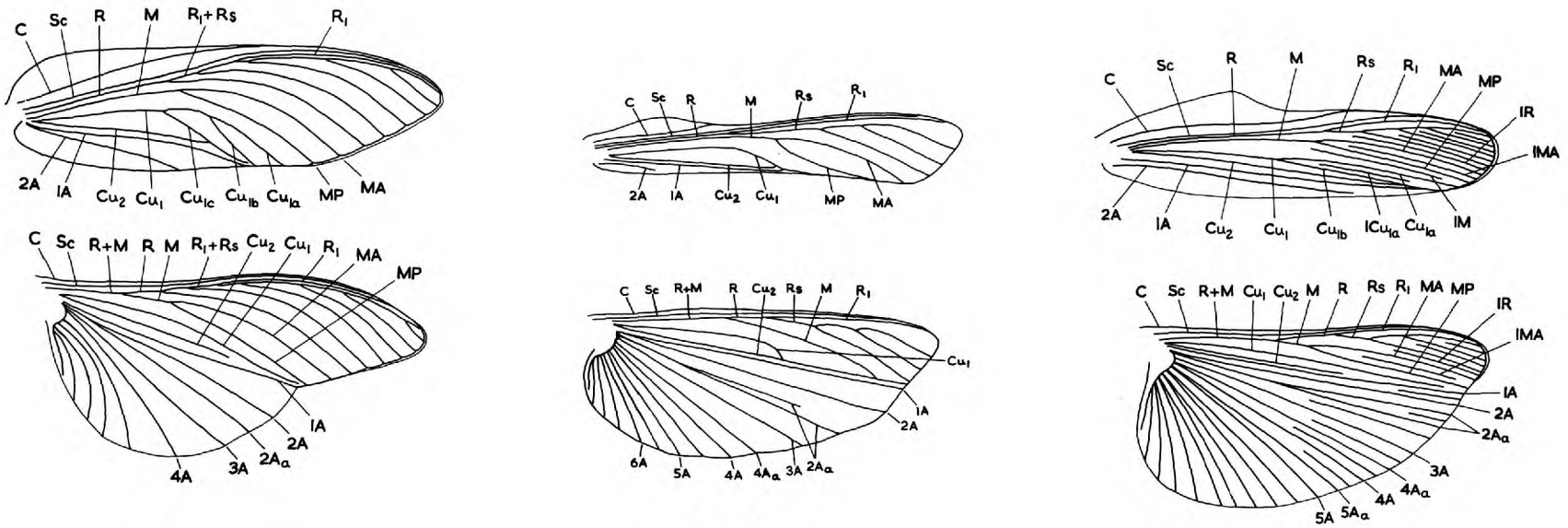
Fig.1. The fore wings of Stenodictya lobata (above) and of a typical Pneumorid.

see p. 31). The wing-venation of the remaining Acridoid families (apart from that of the highly modified Tetrigidae) is easily derivable from the Pneumorid type as shown by the diagrams in Fig. 2.

As this conclusion hangs on the definition of primary veins, it would be as well at this point to make this definition rather more specific. Primary veins are defined on p. 67 as the longitudinal veins of the more primitive fossil wings, and those of them which have persisted in later forms; basal articulation, tracheae, and macrotrichia, ~~were~~ are mentioned as confirmatory characters. For this definition to be satisfactory, it is necessary to specify a standard fossil wing, and this matter will now be dealt with.

It is necessary that this standard fossil wing should be of the type found in the Palaeodictyoptera, as these are the only fossil insects which show no specializations connecting them to any particular modern order. As, generally speaking, modern insects have fewer branches to their wing-veins than the Palaeodictyoptera, the veins of the standard wing should likewise have few branches, so as to facilitate comparison with modern forms. A wing satisfying these requirements is shown in Fig. 3; it is very similar to some of the members of the Dictyoneuridae (e.g. Dictyoneura Goldenberg, Stenodictya, Microdictya Brongniart, Polioptenus Scudder, Goldenbergiana Scudder, Stilbocrocis Handlirsch).

As neither the dichotomous nor the pectinate type of



Shortridgea **Erianthus** **Poecilocerus**

Fig.2. The wings of representatives of the Pneumoridae, Eumastacidae, and Acrididae.

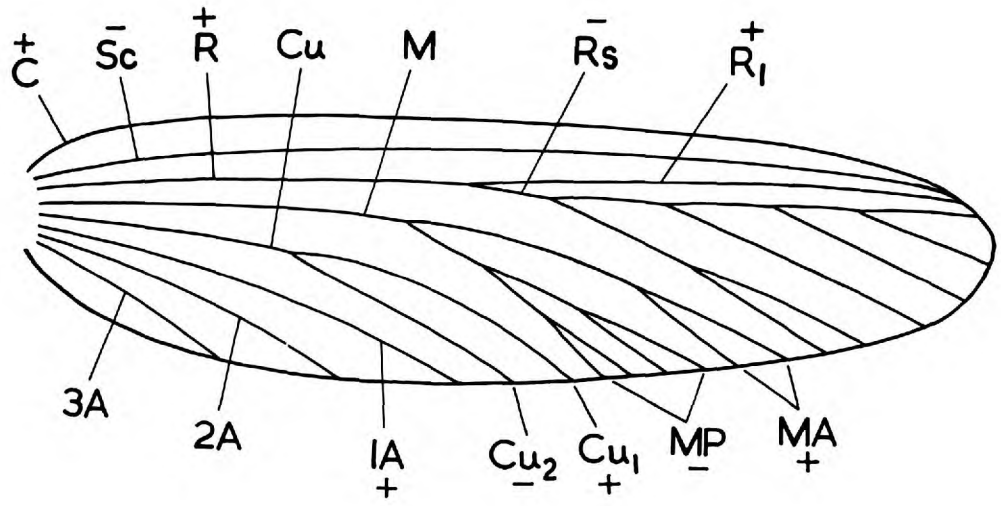


Fig.3. A standard fossil wing (see p.25).

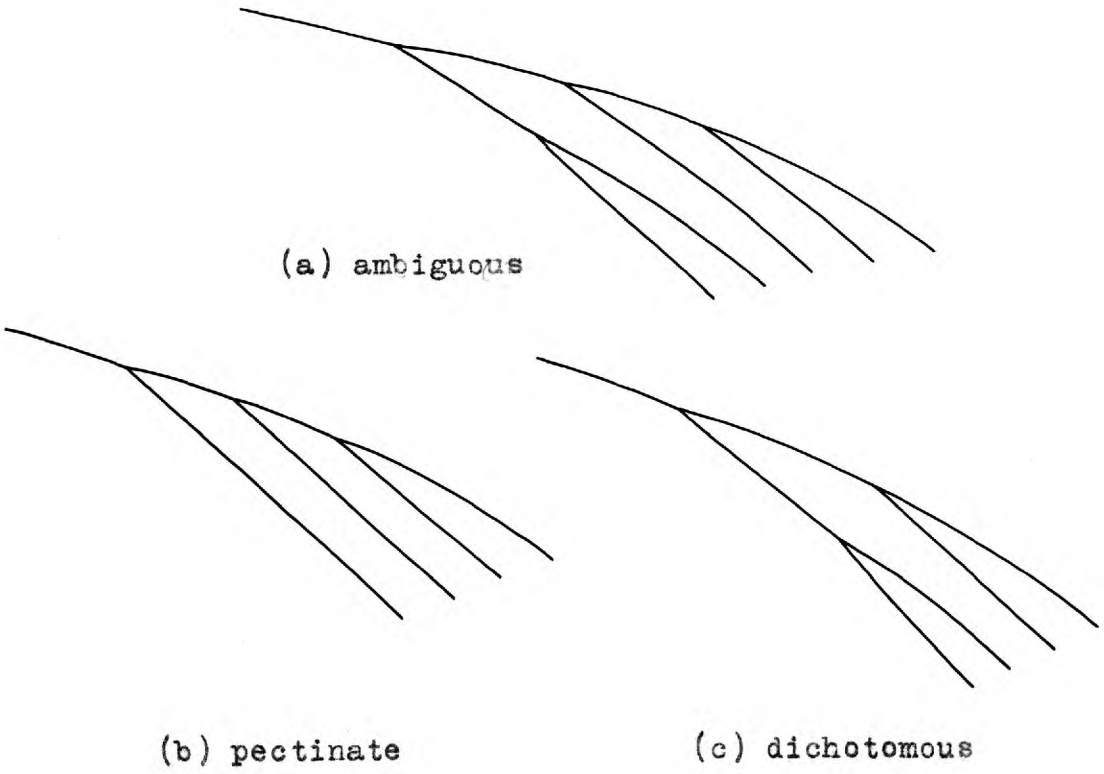


Fig.4. The three main types of radial sector (see p.32).

radial sector had been established at this stage, this vein has been given an ambiguous form (see p.32). It should be mentioned that this standard fossil wing is representative of both fore and hind wings.

If this wing is used as the standard type of primitive fossil wing, the definition of primary veins mentioned above becomes satisfactory, and the wing-veins of such fossil forms as Stenodictya become primary by definition.

To end this Section, the distinction between primary veins and accessory veins (as defined on p.73) will be clarified. Under the Comstock-Needham System, each primary vein is regarded as having a certain primitive form, and, if branched, a certain primitive number of branches. When a primary vein has more than the number of branches specified in this way, the additional branches are looked upon as secondary modifications, and are called accessory veins.

They are of two types: those which are formed by the 'splitting' of primary veins or as outgrowths from them, and those formed from the archedictyon in the same way as intercalary veins. It is accessory veins of the former type which are liable to be confused with primary veins, as they are preceded by tracheae in the nymphal wing-pad.

As most accessory branches of this type no doubt develop in exactly the same way as primary branches, there is no fundamental distinction between the two types. The

difference in this case is phylogenetic rather than morphological, depending on the period in geological history in which the branch was developed. Thus, in general, branches common to all Carboniferous insect wings are regarded as primary, and those found only in some Carboniferous insects or only among modern insects are regarded as accessory. Comstock and Needham placed this distinction on a firmer footing by constructing a hypothetical wing (Comstock, 1918, Fig. 6), exhibiting the probable characters of the wings of an insect ancestral to all modern forms. Any branches not shown in this hypothetical wing they regarded as accessory.

It will be shown later in this Section (p. 32) that the dichotomous, four-branched, radial sector which Comstock and Needham included in their hypothetical wing cannot be regarded as being ancestral to the radial sector of Saltatorial wings. Also, since the work of these two authors, it has been shown (notably by Lameere, 1922) that many fossil wings and some modern ones have an additional branch to the media (called the anterior media, MA). If the venation of Comstock and Needham's hypothetical wing is altered to comply with these two considerations, a venation of the type shown in Fig. 3 is obtained. The subcosta has not been given a two-branched form (as in Comstock and Needham's hypothetical wing) as there is no evidence for this condition being ancestral to the various types of subcosta found in the Saltatoria.

In this work, all additional branches to those shown in Fig. 3 are regarded as accessory, with the exception of those in the anal lobe of the hind wing. The development of this lobe has made it impossible to ascribe definite homologies to the veins supporting it, and the nomenclature applied to the veins posterior to 1A is not intended to suggest any relationships with other orders of insects. The tracheated veins in this region are treated as primary, and those without tracheae as either accessory or intercalary (as defined on p. 73). The second of the first two veins behind 1A in the the Acrididae, Eumastacidae, and Pneumoridae, is regarded as an accessory branch of the first.

When a primary vein, primitively unbranched, becomes divided into two or more equally-developed branches, it is often impossible to regard any one of them as primary and the remainder as accessory. An example of this is Cu_1 in Acridid fore wings. This vein is normally divided into two branches, and sometimes the anterior branch divides again; the resulting three veins (Cu_{1a}, Cu_{1b}, and Cu_{1c}) are formed in exactly the same way and are structurally identical. All branches of this type are referred to in this work as 'pseudo-primary' veins, and are necessarily described in the same place as the primary vein from which they arise.

It should be mentioned in conclusion that the two types of accessory vein mentioned on p. 26 do not correspond

with Comstock and Needham's 'marginal' and 'definitive' types, the latter distinction being one of degree only, and applicable to both tracheated and non-tracheated accessory veins. An example of the latter type, which is much rarer than the former, is $1A_a$ in the Acridid fore wing.

(b) Evidence from present-day forms.

(i) Tracheation.

The primary wing-veins of adult Saltatoria (and many other insect orders) are normally formed round the already-existing tracheae in the wing-pads of the last stage nymphs. The pattern formed by these tracheae is simpler and more regular than that of the adult veins. It is also more primitive, in that most specializations shown by the adult primary veins will usually be undergone to a much less extent (or not at all) by the tracheae. For example, where two veins have fused in the adult, their preceding tracheae will often be separate in the nymph; also, what appears to be a cross-vein in the adult wing may be revealed to be a sudden bend in a primary vein by reference to the tracheation.

Tracheation is, therefore, very useful in determining the homologies of wing-veins. Owing to the time-lag between the development of a specialization in the adult wing and its adoption by the tracheal pattern of the nymphal wing-pad, one often finds that the latter has many features in common with the adult wings of fossil forms related to the insect concerned.

The two sources of evidence provide a mutual confirmation.

Unfortunately, when a vein becomes reduced, its representative trachea in the nymph apparently becomes redundant, and may disappear altogether. This has happened with Cu_2 in many Acrididae, for example, and provides a limitation to the use of tracheation in determining vein homologies.

The tracheation of Acridoid wing-pads normally shows seven main tracheal stems towards the base. Taking these as representing seven primary veins, they may be named C, Sc, R, M, Cu, 1A, and 2A, beginning anteriorly. This conclusion agrees entirely with those arrived at from other sources.

In the anal lobe of the hind wing, this argument leads one to suppose that all the veins behind 1A are branches of 2A, since their tracheae all arise from a single main stem at the base. Or, as this main stem (at least in the Acrididae) divides into two principal branches (from which all the ultimate branches arise), it is possible that both 2A and 3A are present. Or, again, since all the ultimate branches still arise at the base of the wing-pad, one could argue that they all have the status of separate primary veins, and could simply be named 2A, 3A, 4A, 5A, etc.

One objection to the latter argument would be the fact that early fossil hind wings have much fewer anal veins; but if the additional branches were added on behind the already-existing ones (as opposed to arising as branches), and

assuming that they are morphologically and physiologically identical to them, it would seem reasonable to put them all in the same category.

A satisfactory nomenclature for the anal veins evidently cannot be derived from tracheation alone, and further discussion is deferred to the conclusions on p.44 .

(ii) Form.

Throughout the insect orders each primary vein is most commonly found in a particular form, i.e. with or without branches, or branching in a characteristic way. The costa and subcosta, for example, are usually unbranched. If the first two primary veins in an insect wing answer this description (as they do in the Acridoidea), this in itself is a reason for calling them costa and subcosta, respectively.

The criterion of form is most useful in the case of the radius. In many modern and in all fossil orders (with the exception of the Protocoleoptera) the radius has a single anterior branch (R_1) and a subdivided posterior branch (R_s). This posterior branch, the radial sector, may be divided in a pectinate or dichotomous fashion.

There is a primary vein in Acridoid wings which branches in a way typical of a radius with a pectinate radial sector (this condition has been obscured by fusion in some Pneumorids and by reduction in some Acridids). Thus the argument in favour of this vein being the radius would be very

strong using the criterion of form alone, though ample substantiation is in fact supplied by other criteria.

The primitive nature of the branches of the radial sector must now be considered. Comstock and Needham (Comstock, 1918) came to the conclusion that the radial sector of the primordial insect wing was dichotomous and four-branched. This was primarily based on the occurrence of this type of radial sector in the more generalized members of several insect orders. They sought for confirmation for this among the earliest insect fossils, coming to the conclusion that the dichotomous type was much more common than the other.

There is, however, no fundamental distinction between the two types, and the radial sectors in the wings of many of these earliest fossils can be looked upon as both pectinate and dichotomous. A sector of the type shown in Fig. 4a, for example, could be derived equally well from either a pectinate or a dichotomous type (Fig. 4b and c), as could any sector with less than four simple branches. As radial sectors of this ambiguous form are common in the Palaeodictyoptera, it seems clear that neither the pectinate nor the dichotomous type had been established definitely in this order.

The nature of the radial sector in the sufficiently well-preserved genera of this order is shown in the list below:-

FAMILY	GENUS	TYPE OF RADIAL SECTOR
Dictyoneuridae	Stenodictya Brongn.	pectinate
	Microdictya Brongn.	ambiguous
	Titanodictya Handl.	dichotomous
	Polioptenus Scudd.	pectinate or ambiguous
	Dictyoneura Gold.	ambiguous
	Goldenbergiana Scudd.	ambiguous
	Sagenoptera Handl.	ambiguous
	Acanthodictyon Handl.	ambiguous
	Eumecoptera Handl.	pectinate
	Dictyoneurula Handl.	ambiguous
	Stilbocrocis Handl.	ambiguous
	Gegenemene Handl.	ambiguous
Megaptilidae	Megaptilus Brongn.	pectinate
Mecynopteridae	Mecynoptera Handl.	ambiguous
Lithomantidae	Madroneuria Handl.	ambiguous
	Eurythmopteryx Handl.	ambiguous
	Propalingenia Handl.	ambiguous
	Rhabdoptilus Brongn.	ambiguous
Lycocercidae	Lycocercus Handl.	pectinate or ambiguous
	Platephemera Scudd.	ambiguous
Homoiopteridae	Homoioptera Brongn.	ambiguous
	Graphiptiloides Handl.	pectinate

FAMILY	GENUS	TYPE OF RADIAL SECTOR
Homoiopteridae	Homoeophlebia Handl.	ambiguous
	Anthracentomon Handl.	ambiguous
Heolidae	Heolus Handl.	ambiguous
Breyeriidae	Breyeria Borre	ambiguous
	Megaptiloides Handl.	pectinate
	Borrea Brongn.	pectinate
Fouqueidae	Fouquea Brongn.	ambiguous
Graphiptilidae	Graphiptilus Brongn.	pectinate
	Apopappus Handl.	pectinate
Spilapteridae	Palaeoptilus Brongn.	pectinate
	Spilaptera Brongn.	pectinate
	Epitethe Handl.	pectinate
	Campsoneuria Brongn.	ambiguous
	Becquerelia Brongn.	ambiguous
	Homaloneurina Handl.	ambiguous
	Homaloneurites Handl.	pectinate
	Homaloneura Brongn.	pectinate
Lamproptilidae	Lamproptilia Brongn.	ambiguous
Polycreagridae	Polycreagra Handl.	ambiguous
Eubleptidae	Eupleptus Handl.	dichotomous

FAMILY	GENUS	TYPE OF RADIAL SECTOR
Metropatoridae	Metropator Handl.	dichotomous
Paoliidae	Paolia Smith	dichotomous or ambiguous
Stygnidae	Stygne Handl.	ambiguous
Aenigmatodidae	Aenigmatodes Handl.	ambiguous
Incertae Sedis	Bathytaptus Handl.	ambiguous
	Palaiotaptus Handl.	pectinate
	Mecynostoma Brongn.	pectinate
	Pseudohomothetus Handl.	pectinate
	Aedoeophasma Scudd.	ambiguous
	Pseudofouquea Handl.	ambiguous
Syntonopteridae	Syntonoptera Handl.	ambiguous
Orthocostidae	Orthocosta Bolton	ambiguous
Pteronidiidae	Pteronidia Bolton	pectinate
Cryptoveniidae	Cryptovenia Bolton	dichotomous

TOTALS

ambiguous	32 genera
pectinate	17 genera
dichotomous	4 genera
pectinate or ambiguous	2 genera
dichotomous or ambiguous	1 genus

The families shown in this list are those given by Handlirsch in Schröder (1925); the genera are taken from Handlirsch (1908), with the additional ones given by Handlirsch (1911) and Bolton (1912), forming the four new families (the last four in the list above) given in Schröder (1925).

If the genera are subdivided stratigraphically, the following distribution of types of radial sector is obtained (the numbers refer to genera):-

	amb.	pect.	dich.	pect. or amb.	dich. or amb.
Lower Upper Carb.	4	0	1	0	1
Middle Upper Carb.	17	4	3	1	0
Upper Upper Carb.	9	13	0	1	0

If we now ignore the genera which show more than one type of radial sector and consider the <u>proportion</u> of each type in each of these stratigraphical divisions, the following distribution is arrived at:-

	ambiguous	pectinate	dichotomous
Lower Upper Carboniferous	80%	-	20%
Middle Upper Carboniferous	71%	17%	12%
Upper Upper Carboniferous	41%	59%	-

If these figures are plotted the graph shown in Fig. 5 is obtained. If all Carboniferous insects are taken into consideration (thereby increasing the number of sufficiently well-preserved genera from 54 to 122), and the proportions

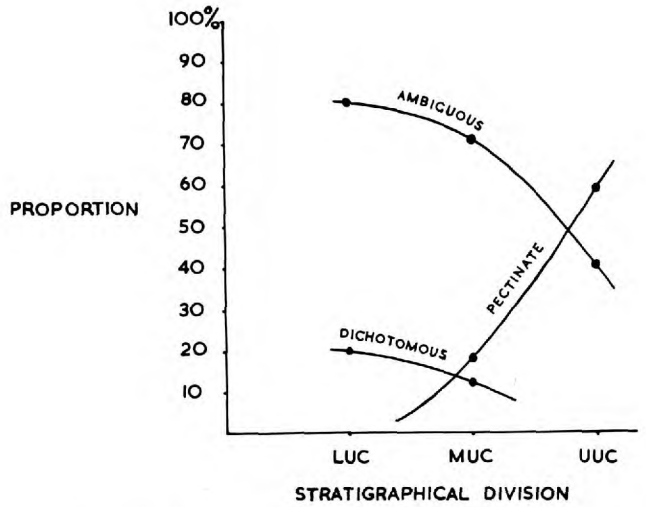


Fig.5. Graph showing the evolutionary trends of the radial sector in the Palaeodictyoptera (see p.36).

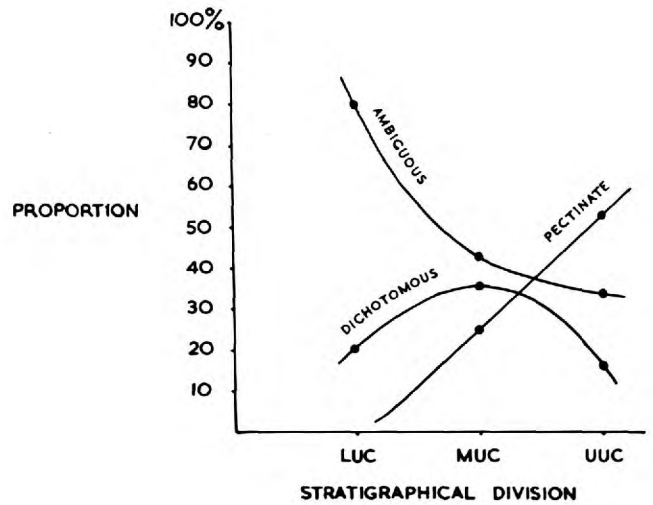


Fig.6. Graph showing the evolutionary trends of the radial sector in all Carboniferous insects (see pp.36 & 37).

again plotted, the graph shown in Fig. 6 is obtained. The additional information for this graph is taken from Handlirsch (1908).

As the number of known fossils is undoubtedly but a small fraction of the actual insect fauna of this period, it is impossible to draw any definite conclusions from these figures. It seems very probable, however, that the ambiguous type of radial sector was most common at the beginning of the Carboniferous period, becoming less common towards the end. The known fossils suggest, therefore, that there was a gradual tendency for the radial sector to assume a definite form, and that, at the end of the Carboniferous period, the assumed form was probably predominantly pectinate.

It is clear from the figures given on p. 35 that in the known Palaeodictyoptera the pectinate type of radial sector is much more common than the dichotomous type, and that radial sectors of indefinite form outnumber both these types. Comstock (1918) regarded all these ambiguous radial sectors as dichotomous, and thus came to the conclusion that the dichotomous form was the most common.

For the purposes of this work it is only necessary to point out that, as the pectinate type of radial sector is more common than the dichotomous type in the known Palaeodictyoptera (and this fossil order approaches the most primitive Acridoid venation more closely than any other), it would be

meaningless to apply a nomenclature to the pectinate branches of this vein in the Acridoidea based on the supposition that their original form was dichotomous. Partly because of this, and partly because no obvious purpose would be served by it, these branches have not been given individual names in this work.

It would be as well at this point to correct a rather misleading statement made by Comstock. Referring to the Neuroptera, he states (Comstock, 1918, p. 147) that the pectinate radial sector 'is a distinctive characteristic of this order; in no one of the other orders of living insects in which accessory veins occur is a well-developed pectinately branched radial sector found'. The great exception to this is the Orthoptera Saltatoria, in which the form of the radial sector (when sufficiently branched to show one form distinct from the other) is always pectinate, and in which accessory veins are common.

The form of the media and cubitus is not very distinctive: one can only say that they normally branch at least once. More than two branches are common in the case of the media, but much rarer in the case of the cubitus. In the Acridoidea, the media (as defined by its position) is generally simply bifurcate. Occasionly it is unbranched, and rarely three-branched. The cubitus (as defined by its position) is always bifurcate at or very near its base, and the anterior

branch sometimes divides again in the fore wing. Thus, in the case of these two veins, form can only be regarded as faintly confirmatory.

The anal veins of insect wings are almost always unbranched. In Acridoid fore wings, the primary veins behind the cubitus are normally unbranched, and thus their identity with the anal veins (easily established on other grounds) is to some extent confirmed. As has been discussed elsewhere (pp. 30, 31, and 45), it is impossible to be definite about the homologies of the veins in the anal lobe of the hind wing, and, as this region has undergone so much modification, the criterion of form is here useless.

(iii) Position.

This criterion is of considerable importance in determining the homologies of primary veins. As soon as the primary nature of a vein has been established, its position in the wing is often sufficient for its homology to be determined. For instance, the most anterior primary vein must be the costa, the third primary vein from the anterior margin must be the radius, and so on. If there are grounds for supposing that one or more of the primary veins is missing, or that fusion between two of them has taken place, this must naturally be taken into account. In primitive fossil wings, the primary nature of the wings is established by definition, and their position thus becomes a definition of their identity; this also applies to modern wings, when comparison with fossil

venation is both easy and justified.

This method of vein identification can be applied quite easily to the most primitive Acridoid venation, that of the Pneumoridae. Here, the only difficulty that can arise in the fore wing concerns the cubitus, the two main branches of which arise so near the wing-base that, using the criterion of position alone, they could be regarded as independent primary veins. A closer examination, however, shows this to be incorrect, and this is confirmed by tracheation. In the hind wing, a similar argument applies to the cubitus, but additional difficulties arise from the basal fusion of R and M, and the development of the anal lobe. That fusion between M and R has taken place is shown by tracheation and comparison with the fore wing; no definite homologies can be applied to the veins posterior to 1A in the hind wing, as discussed on pp. 30, 31, and 45 .

It is clear that the more specialized a wing is the more difficult it is to deduce homologies from the position of the veins alone, and this criterion would be of little use in identifying the veins of some of the more highly specialized Acridine wings.

(iv) Convexity and concavity.

In many early fossil wings (notably those of the Palaeodictyoptera), the branches of the veins are alternately raised and depressed, thus giving the wing a corrugated appearance. The correspondence between the identity of the

vein and its convexity or concavity is constant in these early forms, and is shown in Fig. 3. This correspondence has persisted to a varying extent in some modern orders, and is therefore sometimes useful in confirming vein homologies. In many present-day forms, however, the convexities and concavities (when developed at all) are modified or even reversed, and there are serious limitations to using this criterion in other than a confirmatory capacity.

In most Acridoid wings, very few of the original convexities and concavities are retained. Pneumorid wings are nearest to the primitive form in this respect; the usual convexities and concavities of their veins are shown in Fig. 7. It will be seen in the fore wing that what convexities and concavities are developed are of a primitive nature. They are largely confined to the base of the wing, which becomes flattened towards the apex. This is also true of the hind wing, in which a very large part of the pre-anal area is flattened. The cubital branches sometimes show the opposite of their primitive convexity and concavity in the hind wing, and this is occasionally true of the branches of the media.

In the other Acridoid families, these modifications are carried further, and the criterion is of little use. For a possible explanation of the trend of the convexities and concavities in the Acridoidea, see p. 87 .

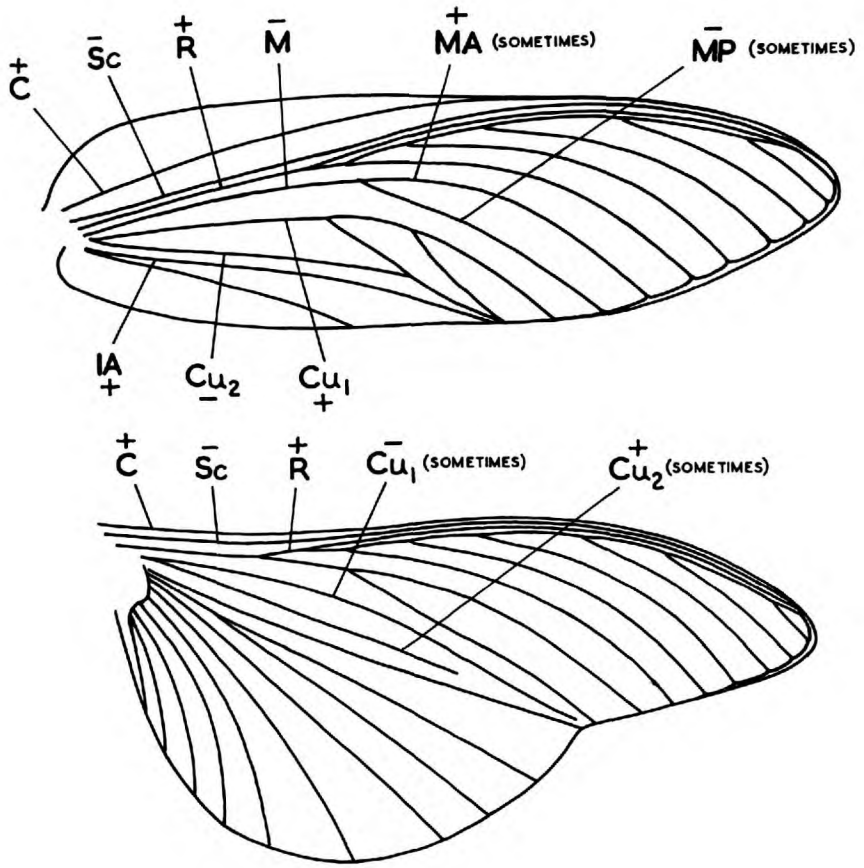


Fig.7. The convexities and concavities of Pneumorid wing-veins.

(v) Basal articulation.

The arrangement of the veins at the base of the wing, and their articulation with the axillary sclerites, is sometimes useful in determining their homologies. Particularly is this so when a comparison is made between the fore and hind wings. The Acridoid wing-base is rather modified in that C and Sc are typically fused together at the base, and M and Cu have to a large extent lost their connection with the distal median plate. Thus this criterion has not been of much use, except in assisting with comparison between the fore and hind wings, and in confirming the primary nature of the veins involved.

(vi) Macrotrichia.

Primary veins typically bear macrotrichia on their dorsal surface. A good example of this is shown by the fore wing of Locusta migratoria Linnaeus, in which the macrotrichia are normally entirely confined to the primary veins. This criterion, however, is very unreliable, as primary veins frequently have no macrotrichia, and the latter are sometimes found on secondary veins. Macrotrichia are of no use, of course, in distinguishing one primary vein from another, but merely suggest whether or not a vein is primary.

(c) Mutual confirmation.

In practice it is unsound to base any conclusions on a single criterion when others are available. All the criteria

discussed above are confirmatory to some extent, and it is only when several of them are in agreement that homologies can be ascribed to veins with any certainty.

The characteristic form of the radius, for example, is indirect evidence for its being a primary vein; the identity of the subcosta is made more certain if it is considered as being between an unbranched vein and a vein with a pectinate sector, rather than being looked upon merely as the second primary vein.

The validity of the conclusions summarized below rests on this agreement between criteria which are in themselves of a confirmatory nature, but which by mutual confirmation provide a sound basis for the determination of homologies.

In the above discussion on the reasons for the application of the nomenclature proposed in this work, it has been necessary to use the term 'primary vein' from time to time. It may be thought that this was in some cases begging the question, but the term was only applied when most of the criteria were in agreement with this course, an anticipation of the conclusions which obviated the temporary use of another term.

(d) Summary of conclusions.

It is proposed to give under this heading a brief summary of the reasons for the application of each name to the primary veins of Acridoid wings. A separate account is given for each vein, beginning anteriorly.

THE COSTA

That this is a primary vein is shown by tracheation and basal articulation, often confirmed by macrotrichia. Its identity as the costa is established by its position (especially in the hind wing, where it forms the leading edge) and form, confirmed by its convexity in the hind wing.

THE SUBCOSTA

A primary vein because of its trachea and basal articulation, often confirmed by macrotrichia. Subcosta because of its position and form, confirmed by its concavity in the hind wing.

THE RADIUS

A primary vein because of its trachea and basal articulation, often confirmed by macrotrichia. Radius because of its position and highly characteristic form, confirmed by its convexity.

THE MEDIA

A primary vein because of its trachea, often confirmed by macrotrichia. Media because of its position, confirmed by its form. There is no evidence to show that either the primitive anterior branch (MA) or posterior branch (MP) is

is missing (for a full discussion see p. 69).

THE CUBITUS

A primary vein because of its trachea, often confirmed by macrotrichia. Cubitus because of its position, confirmed by its form (see p.87 for additional remarks concerning Cu_2).

THE FIRST ANAL

A primary vein because of its trachea and basal articulation, often confirmed by macrotrichia. First anal because of its position, confirmed by its form.

THE REMAINING ANALS

In the fore wing, the second anal is a primary vein because of its trachea and basal articulation, often confirmed by macrotrichia. It is the second anal vein because of its position, confirmed by its form.

As indicated on pp. 30 and 39, there is insufficient evidence for applying definite homologies to the veins behind 1A in the hind wing, as the development of the anal lobe has obscured their affinities. It is possible that these veins are divisible into two groups, representing 2A and 3A, respectively. Or 2A and 3A may be individual veins among them, the remainder being of a secondary nature. As there is no sound basis for definite conclusions, an arbitrary system has been used, the details of which are given on p. 28.

The reasons set forth in this summary apply more

particularly to the Pneumoridae, in which the most primitive Acridoid venation is found. From this type of venation it is easy to derive the more specialized forms found in other Acridoidea.

2. THE TETTIGONIOIDEA

(a) Evidence from fossil forms.

The fossil history of this group is rather better known than that of the Acridoidea, but is still too incomplete for lines of evolution to be traced with any certainty. It is quite probable that some of the Protorthoptera are closely related to the ancestral line of the Tettigonioidea, especially the families Pachytylopsidae, Caloneuridae, Oedischiidae, and Sthenaropodidae. Zeuner (1939) has in fact suggested that these families could be regarded as Saltatoria. As this author has discussed the fossil Tettigonioidea in some detail, the following account is made as brief as possible.

The most primitive Tettigonioid wing-venation is found in the fossil members of the families Prophalangopsidae and Gryllacrididae. In the former family, the most primitive form known is Hagla gracilis Giebel (Fig. 8). In the Gryllacrididae, the venation of the most primitive fossil forms is badly preserved, but it is probable that the typical venation resembled that shown in Fig. 9. The venation of the fore wings of the Protorthopteran forms most likely to be

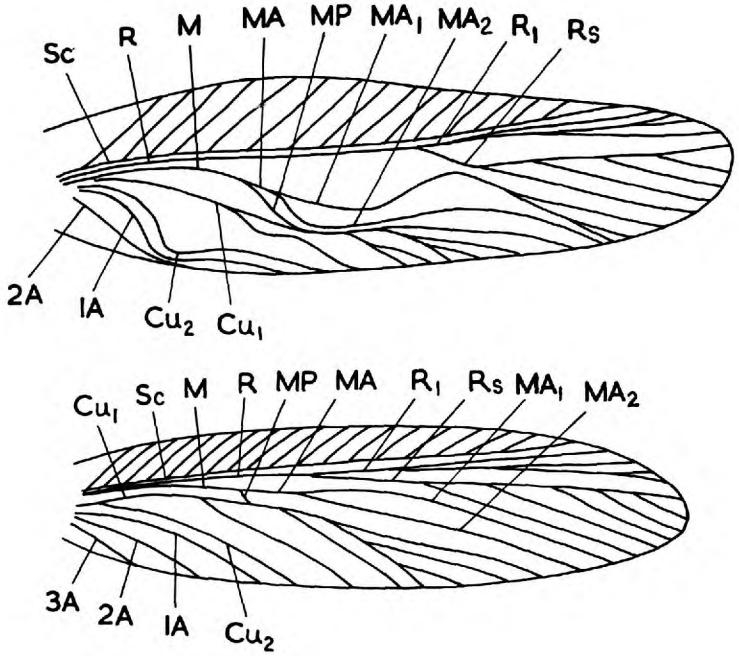


Fig.8. The male (above) and female fore wings of Hagla gracilis.

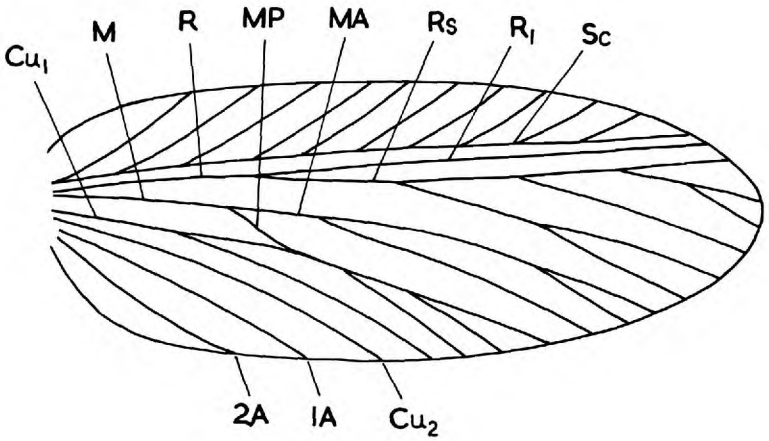


Fig.9. The typical wing-venation of fossil Gryllacridid fore wings.

related to the Tettigonioidea is shown in Figs. 10, 11, 12, and 13.

On the basis of these figures it is possible to assess the likelihood of the Tettigonioidea being derived from Protorthopteran stock. It will be noticed that in Oedischia Brongniart , Sthenaropoda Brongniart, and Permacridites Martynov, the subcosta bears anterior accessory branches and a certain amount of fusion has taken place between the media and cubitus. These features are both characteristic of Tettigonioid fore wings. The anterior accessory branches of R_1 (also characteristic of primitive Tettigonioid wings) are found in all these forms except Permacridites. The venation of the Caloneuridae and Pachytylopsidae is more primitive, providing a possible link with the early Palaeodictyoptera.

There is no important difference between the venation of the Palaeorehniinae and the Sthenaropodidae, and it is probable that these two groups are fairly closely related. This also applies to the female fore wings of Hagla; in the male, however, there is a certain amount of further specialization near the base of the wing, probably associated with stridulation (the distinction between 'male' and 'female' is based on this fact).

If the diagrams of the venation of Thoronysis Ammon, Caloneura, and Permacridites, are compared with the standard fossil wing (Fig. 3), it will be seen that the correspondence

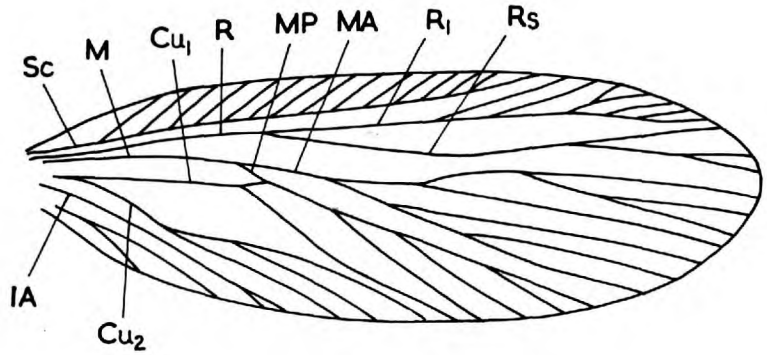


Fig.10a. The fore wing of Sthenaropoda bruesi (Meunier) (Sthenaropodidae). Partly after Vignon (1929).

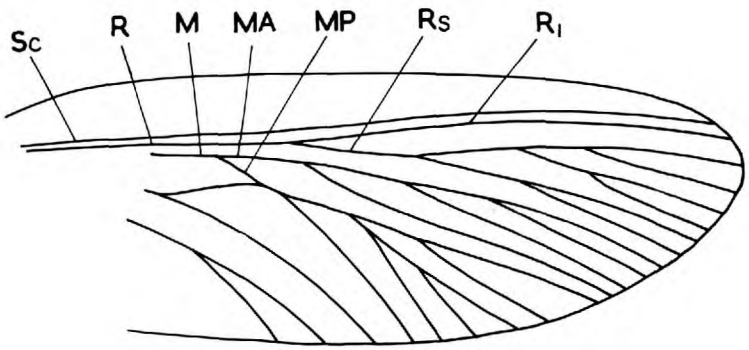


Fig.10b. The fore wing of Permacridites maximus Martynov (Sthenaropodidae). Partly after Martynov (1930).

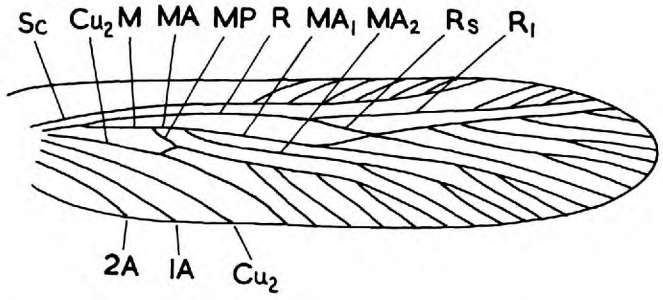


Fig.11. The fore wing of Oedischia williamsoni Brongniart (Oedischiidae). Partly after Handlirsch (1906).

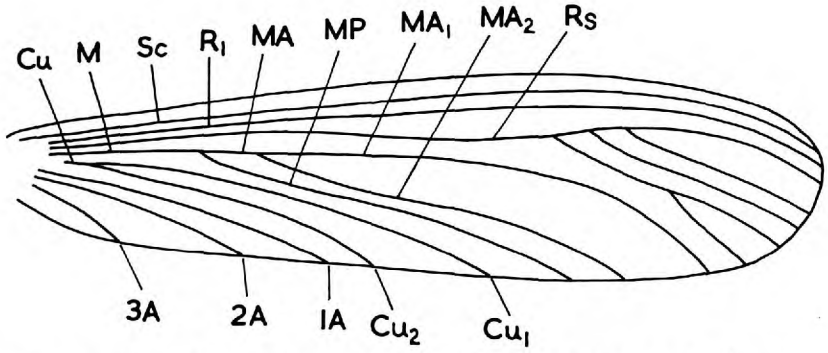


Fig.12. The fore wing of Caloneura subtilis Bolton (Caloneuridae). Partly after Bolton (1925).

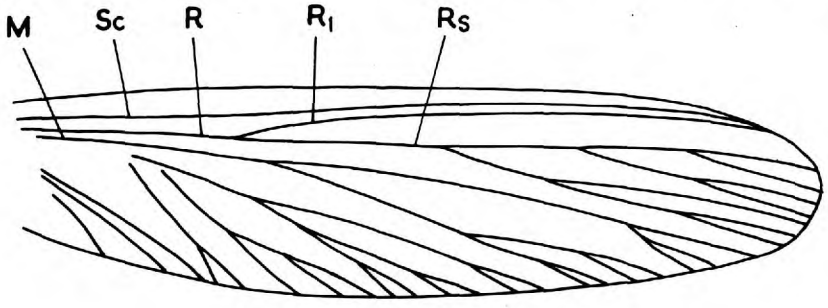


Fig.13. The fore wing of Thoronysis ingbertiensis Ammom (Caloneuridae). Partly after Handlirsch (1906).

is close enough for there to be no doubt that the homologies given to the wing-veins of these genera are correct. Similarly, the derivation of Palaeorehniine and Hagline venation from that of Permacridites is perfectly straightforward.

The modern Gryllacridid venation could easily have arisen from that of the Palaeorehniinae (cf. Figs. 9 and 39). The only difficulty arises in connection with MP. This vein is clearly developed in Permacridites, but its existence is by no means proven in the Palaeorehniinae. The basal stem of this vein is invisible in Palaeorehnia scotica Zeuner, and could not be said to be definitely present in the fore wing of Jurassobatea gryllacroides Zeuner. Its presence in the fore wings of this subfamily can only be established on the basis of its occurrence in Palaeorehnia maculata Cockerell; in the fore wing of this species it is clear and slightly concave. The only other winged Gryllacridid fossil is Macrelcana ungeri (Heer), in which there is no basal stem representing MP; this wing, however, appears to be more highly specialized than the modern Stenopelmatinae. In Sia ferox Giebel, and Stenopelmatus sartorianus Saussure (the only modern winged Stenopelmatinae), this basal stem is also not shown. In some other modern Gryllacrididae (Diaphogryllacris translucens (Serville), Dictyogryllacris dyscrita (Karny)) a structure somewhat resembling the basal stem of MP is developed, but this is very probably brought about by a secondary fusion, as suggested by

Zeuner (1939).

The evidence supplied by these features is far from conclusive; the only Gryllacridid fore wing in which MP can be clearly shown to be present is that of Palaeorehnia maculata, and as this species is only known by one wing fragment it is not even certain that it is a Gryllacridid. However, as no other evidence is forthcoming, it seems reasonable to suppose for the time being that the basal stem of MP shown by Palaeorehnia maculata and Permacridites maximus Martynov has been lost in the fore wings of the modern Gryllacrididae (possibly due to the longitudinal veins becoming arranged in closely parallel lines to facilitate wrapping the wings round the body). If this is true, the media in modern Gryllacrididae is represented only by MA in the fore wing. In the hind wing, the contribution made by fossil evidence is very small: the only fossil Gryllacridid hind wing (that of Jurassobatea) is badly preserved. The only point worthy of note is that the media appears to be three-branched and free from both the radius and the cubitus, all these primitive features being lost in most modern Gryllacrididae.

The venation of the female fore wings of Hagla (see Fig. 8) can also be easily derived from that of Permacridites. The specializations in the male venation consist mainly of a marked undulation of the veins posterior to R. Cu_2 touches 1A at one point. The derivation of the remaining Prophalangopsidae

from Hagla also presents no difficulty. The rôle of Zalmona brodei Giebel and Termitidium ignotum Westwood in providing venational schemes intermediate between the Prophalangopsidae and Tettigoniidae has been fully dealt with by Zeuner (1939) and need not be discussed here.

There is one point of interest in Prophalangopsid hind wings: this is the development of the anterior branch of Cu_1 and its fusion with MP. There are only two fossil hind wings which help in this matter, those of Hagla gracilis (Fig. 35) and Pamphagopsis maculata Martynov (Fig. 36). In the former species this anterior branch (Cu_{1a}) is not developed, whereas in the latter it is. In the hind wing of Prophalangopsis, one of the apparent cross-veins between Cu_1 and MP is rather more strongly developed and oblique than the others, and may represent the basal stem of Cu_{1a}. This vein is very characteristic of Tettigoniid hind wings, and it seems likely that it was first developed in the Prophalangopsidae.

The remaining family to be considered is the Elcanidae. The supposed relationships of this fossil family are in a constant state of flux. Handlirsch (1908) considered them as Ensiferoid but allied to the Locustopsidae. Karny (1930) regarded both these families as being subfamilies of the Gryllacrididae. Jeannel (1949) - basing his views largely on Martynov's work - maintains that the Elcanidae are a side branch of the Oedischiidae, which he supposes arose

from early Acridoid stock. Jeannel (op. cit.) also supports Martynov's view that the Locustopsidae are a side branch from Tettigoniid stock.

The venation of a typical species of Elcana is shown in Fig. 14. The concave subcosta and the radius with a convex R_1 are easily recognized. The vein immediately behind the radius must be the media; it gives rise to a convex anterior branch (MA) and a concave posterior branch (MP). MA divides again, and the anterior branch MA_1 touches the base of R_s. That this is a correct interpretation is confirmed by some specimens in which MA_1 and R_s do not quite touch (e.g. I. 10452 and I. 10706, Brit. Mus. (Nat. Hist.) Collection), being connected instead by a short cross-vein. Behind the media is a two-branched cubitus; Cu_1 is convex, and Cu_2 concave. There are one or two anal veins, and the costa is represented by one or both of the veins anterior to Sc. The convexities and concavities referred to above may be observed clearly on specimen I. 3376.

The resemblance between this venation and that of the Locustopsidae has long been recognized, though in fact there are important differences in many respects. Some characteristics of Elcanid fore wings not found in the fore wings of the Locustopsidae are listed below:-

1. The costa normally bears no anterior accessory branches of the Locustopsid type.

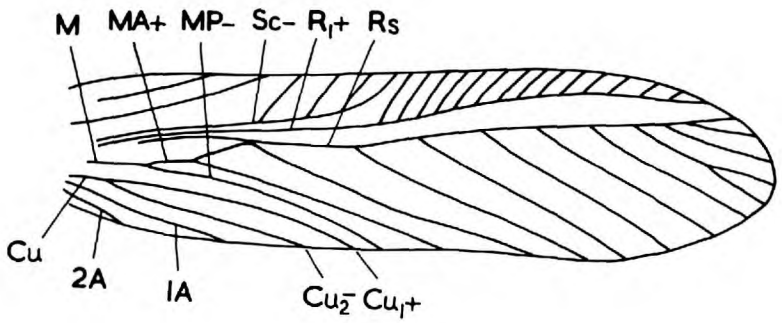


Fig.14. The fore wing of a typical species of Elcana.

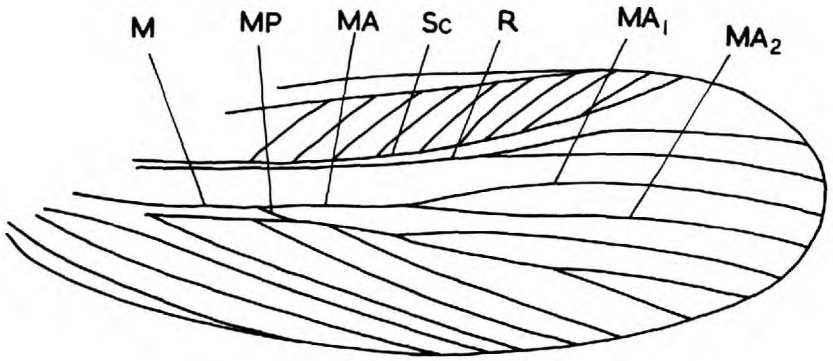


Fig.15. The female fore wing of Mesogryllus achelous (Westwood).

2. The subcosta is much shorter, being only about half the wing-length, compared with the Locustopsid Sc, which reaches to near the apex of the wing.
3. R_1 gives rise to numerous accessory branches.
4. The bifurcation of the radius is much nearer the base of the wing.
5. The radial sector occupies a much larger area of the wing and has many more branches.
6. MA_1 usually touches R_s.
7. The bifurcation of M is much nearer the wing-base.
8. Cu_1 is unbranched.
9. There is a much greater number of primitive convexities and concavities.
10. The bifurcation of Cu is some distance from the wing-base.
11. The wings are relatively broader.

When these differences are taken into account, it seems unlikely that the two families are closely related. Other features of the body tend to confirm this, as the Elcinidae have long antennae, a large external ovipositor, and an appearance generally suggestive of the Tettigonioidea. Their only feature which could be regarded as Acridoid is the hind femur, which appears to be carinate. The Locustopsidae have not got a long ovipositor, and no long antennae are

visible on the specimens which Zeuner (1942) has examined.

There is insufficient evidence for any sound phylogenetic conclusions regarding the Elcanidae. They are here regarded as Tettigonioidea because of the antennae and ovipositor; the venation suggests that they arose from Protorthoptera in which the fusion of Cu_1 and MP had not yet taken place

(b) Evidence from present-day forms.

(i) Tracheation.

As in the Acridoidea, Tettigonioid wing-tracheation usually shows seven main tracheal stems, and when these are named C, Sc, R, M, Cu, 1A, and 2A, there is complete agreement with conclusions arrived at from the other sources of evidence. The costal and subcostal tracheae generally arise from a short common trunk at the base - at least in the later instars, as in the Acridoidea. More than two anal tracheae are often found in Gryllacridid fore wing-pads, and this was doubtless also true of the Prophalangopsidae. The tracheae in the anal lobe of the hind wing-pad are discussed on p. 30.

(ii) Form.

This criterion agrees in general with conclusions derived from fossil evidence, tracheation, and position. The costa (as deduced from the latter three criteria), however, is branched in some fore wings, particularly in the Gryllacrididae, and it is characteristic of both the Prophalangopsidae and Tettigoniidae that the subcosta bears a number of

anterior accessory branches in the fore wing. Accessory branches are also found on R_1 in the Prophalangopsidae and Gryllacrididae, and (in the fore wing) on MA in the Tettigoniidae. Although this extensive accessory branching detracts from the value of form in the Tettigonioidea, this criterion is nevertheless of importance, especially as the accessory branches are generally confined to the fore wing.

The identification of the radius may always be confirmed by its pectinately branched radial sector, a feature found throughout the Tettigonioidea. There is nothing in the form of the media and cubitus to suggest that the application of these names is incorrect.

(iii) Position.

The homologies attributed to the veins of the fore wing of Hagla on palaeolontological grounds (see p. 49) are fully confirmed by the position of the veins. This, of course, is only to be expected, as this criterion defines the nomenclature given to the standard fossil wing, from which the Hagla wing has been derived via the Sthenaropodidae.

Among the modern Tettigonioidea, the criterion of position becomes increasingly less useful as the venation becomes increasingly more specialized. Fusions between R, M, and Cu, have been shown by tracheation studies to be common in both the Tettigoniidae and Gryllacrididae, and it is only when these are taken into account that the position of the

veins becomes elucidated. However, when the primary veins have been satisfactorily delimited, there position does confirm the homologies given to them using other criteria.

(iv) Convexity and concavity.

What convexities and concavities are shown by the wings of fossil Prophalangopsidae agree in general with the homologies ascribed to the veins on the basis of other criteria. Thus Sc is usually concave and R (and R_1) convex. In Cyrtophyllites musicus Handlirsch (type) 1A is convex and Cu_2 concave. Some of the females of Hagla gracilis (e.g. I. 10660, Brit. Mus, (Nat. Hist.) Collection) have a convex Cu_1 and concave Cu_2. In the fore wing of Prophalangopsis obscura (Walker) Cu_2 is concave and 1A convex. The hind wing of this species has a convex C, concave Sc, convex R, and convex 1A.

In the Elcanidae the corrugation of the fore wing is remarkably primitive (see p. 51). The Gryllacrididae have lost most of their convexities and concavities. In the fossil form Palaeorehnia maculata MA is slightly convex and MP slightly concave at their bases. Among modern Gryllacrididae, there is sometimes a tendency for C and R to be convex and Sc concave in the fore wing.

In the Tettigoniidae the fore wing has become largely flattened, but the costa is often slightly convex, the subcosta concave, and the radius almost invariably convex. In the hind wing C and R are always convex and Sc concave.

The criterion of convexity and concavity, then, is too unreliable in modern Orthoptera to be of great use in itself, but often provides a confirmation of conconclusions arrived at from other evidence.

(v) Basal articulation.

The wing-base of the Tettigonioidea is generally rather more modified than that of the Acridoidea, and is of practically no value in determining the homologies of the veins. As there is often very considerable fusion between veins before the axillary sclerites are reached, it is to a large extent impossible to associate any of these sclerites with any particular vein. It should be mentioned, however, that the basal vein-complex of which the radius (as determined by other criteria) is the main component normally articulates with the second axillary sclerite, in both pairs of wings, thus providing another confirmation of the identity of this vein.

This criterion is, of course, useful in confirming the primary nature of a vein, the possession of a basal articulation being characteristic of this type of vein.

(vi) Macrotrichia.

This criterion is of no use in the Tettigonioidea as macrotrichia (when developed) are not confined to the primary veins.

(c) Summary of conclusions.

THE COSTA

That this is a primary vein is shown by tracheation

and basal articulation. It is the costa because of its position and form, confirmed by its convexity in the hind wing.

THE SUBCOSTA

A primary vein because of its trachea and basal articulation. Subcosta because of its position and form, confirmed by its concavity in the hind wing.

THE RADIUS

A primary vein because of its trachea and basal articulation. Radius because of its position and form, confirmed by its convexity.

THE MEDIA

A primary vein because of its trachea, often confirmed by its basal articulation. Media because of its position, confirmed by its form. It seems probable on palaeolontological grounds that the posterior media (MP) has been lost in modern Gryllacrididae, but in the other Tettigonioid families there is no evidence to show that either MA or MP is missing, and the media is therefore regarded as complete.

THE CUBITUS

A primary vein because of its trachea, confirmed by its basal articulation. Cubitus because of its position, confirmed by its form.

THE FIRST ANAL

A primary vein because of its trachea, often confirmed by basal articulation. First anal because of its

position, confirmed by its form.

THE REMAINING ANALS

In the fore wing the second anal is a primary vein because of its trachea and basal articulation. It is the second anal because of its position, confirmed by its form.

For the veins posterior to 1A in the hind wing, the same remarks as those given for the Acridoidea apply (see pp. 45 and 28).

3. THE GRYLLOIDEA

(a) Evidence from fossil forms.

As has been suggested and discussed by Zeuner (1939), it is probable that the Grylloidea are an offshoot from the Tettigonioid line at or just before the level of the Prophalangopsidae. This supposition is largely based on the evidence provided by the fossil subfamily Protogryllinae, and more particularly on the genus Mesogryllus. This genus is known only by female fore wings, the venation of which is shown in Fig. 15. As the phylogenetic significance of this venation is fully discussed by Zeuner (op. cit.), it need only be stated here that the venation of Mesogryllus is intermediate in many respects between that of Hagla and that of the higher Gryllidae. The genus Protogryllus has a rather more specialized venation than Mesogryllus, though occurring in earlier beds.

An interesting feature of the Mesogryllus wing is the presence of a distinct MP, which fuses with Cu_1 for a

short length. Zeuner (op. cit., p.91) believed the basal stem of MP to be present in Protogryllus as well, but this cannot be stated definitely on the basis of the specimens in the Brit. Mus. (Nat. Hist.) Collection, as a clear MP is shown by none of them. If a wing of the Mesogryllus type was directly ancestral to the modern Gryllidae, it would be possible that the media of these modern forms represents MA only, MP having been completely incorporated into Cu_1. This cannot, however, be established on the basis of a single fossil wing, and the media is regarded in this work as complete.

The stridulatory modifications of the male fore wings of the modern Gryllidae can be looked upon as a further development of those shown by the Prophalangopsidae. The sigmoid curve of Cu_2 and 1A is more highly developed, and some of the cross-veins between Cu_1 and Cu_2 have been retained to form the 'harp'. The 'mirror' has been developed from some of the accessory branches of Cu_1; in Protogryllus the mirror is rudimentary, though the harp is quite well developed.

The wing-venation of the Gryllotalpidae is very similar to that of the Gryllidae, and there can be no doubt about the correspondence between the various veins. The harp is fairly well developed in the male but there is no distinct mirror.

Thus there is much evidence in favour of the Gryllid and Gryllotalpid wings being derived, via the Protogryllinae,

from those of the Prophalangopsidae. The derivation of the Prophalangopsidae from Protorthopteran stock (and hence from the Palaeodictyoptera) has been discussed on p. 49.

(b) Evidence from present-day forms.

(i) Tracheation.

There are only six main tracheal stems in the wing-pads of Grylloid nymphs. There is, however, ample evidence in favour of this being due to the loss of the costal trachea or its fusion with trachea Sc. This conclusion is supported by the criteria of fossil evidence and form. The first five tracheal stems may, therefore, be named Sc, R, M, Cu, and 1A, resulting in complete agreement with conclusions arrived at from other sources of evidence. Tracheae 2A, 3A, etc., arise from a common tracheal stem at the base, as in other Orthoptera. Where the first branch of the subcostal trachea has a distinct appearance from the remainder, it is looked upon in this work as the costal trachea.

(ii) Form.

Grylloid fore wings have a highly modified venation, especially in the male, and the criterion of form is not therefore very useful. In the hind wing, however, the venation is not so specialized, and the form of the veins agrees in general with their identity deduced from other criteria. The costa and subcosta are unbranched, R is divided into R_1 and R_s, the media and cubitus are bifurcate

(Cu_1 dividing again), and the anal veins are normally-developed.

In the fore wing the subcosta bears the numerous accessory branches characteristic of the related Prophalangopsidae and the anal veins are fairly normal, but the remaining veins are generally reduced or modified.

The criterion of form, then, is of little use in the fore wing, but provides a confirmation of the homologies ascribed to some of the veins of the hind wing.

(iii) Position.

Once the identity of the subcosta has been established in the fore wing (on the basis of fossil evidence and form), the remaining veins may be named according to their position and the result agrees with conclusions arrived at from other criteria.

This is also true of the hind wing, when allowances are made for the fusions revealed by tracheation.

(iv) Convexity and Concavity.

Grylloid wings have lost most of their primitive corrugation, in common with other Orthoptera, and this criterion is not therefore very useful. The convexities and concavities of C, Sc, and R, in the hind wing confirm their identity, and this is also true of Sc and R in the fore wing, though the corrugation here is much less well-marked.

(v) Basal articulation.

The basal region of Grylloid wings is very much

modified, especially in the hind wing, and the axillary sclerites provide little evidence for determining the homologies of the veins. In the fore wing, the base of the subcosta articulates with the first axillary, and that of the radius with the second axillary, but this should be regarded as a confirmation of the identity of the sclerites rather than of the veins.

In the hind wing, the bases of C, Sc, R, M, and Cu, are not clearly separate and no inferences are possible.

The criterion of basal articulation has, of course, its usual ~~use~~ value in establishing the primary nature of the veins involved.

(vi) Macrotrichia.

As in the Tettigonioidea, the macrotrichia on Grylloid wings (when present) are not confined to the primary veins and are therefore of no use in confirming homologies.

(c) Summary of conclusions.

THE COSTA

See the remarks on pp. 157 and 167 .

THE SUBCOSTA

A primary vein because of its trachea and basal articulation. Subcosta in the hind wing because of its position, confirmed by its form and concavity. In the fore wing, the identity of this vein is established by its position (fossil evidence and form confirming that the costa is lost or incorporated in the subcosta), confirmed by its

form and slight concavity.

THE RADIUS

A primary vein because of its trachea, confirmed by its basal articulation. Radius because of its position, confirmed by its convexity.

THE MEDIA

A primary vein because of its trachea, sometimes confirmed by its basal articulation. Media because of its position, confirmed by its form in the hind wing (and sometimes in the fore wing). For the nature of its branches, see pp. 58 and 59.

THE CUBITUS

A primary vein because of its trachea and basal origin. Cubitus because of its position, confirmed by its form.

THE FIRST ANAL

A primary vein because of its trachea and basal articulation. First anal because of its position, confirmed by its form in the fore wing and the characteristic nature of its trachea in the hind wing.

THE REMAINING ANALS

In the fore wing, the second and third anals are primary veins because of their tracheae and basal articulation, and are thus named because of their position.

For the veins posterior to 1A in the hind wing, the same remarks as those given for the Acridoidea apply (see pp. 45 and 28).

VII. ACRIDOIDEA - LOCUSTOPSIDAE

This fossil family has been the subject of recent paper by Zeuner (1942). This author discusses the venation in some detail, and gives diagrams in which the interpretation of the wing-veins differs in no respect (other than the use of the symbols CuA and CuP for Cu_1 and Cu_2) from that used in the present work. It will suffice, therefore, to give a labelled diagram of the venation of a typical Locustopsid fore wing (Fig. 16); the hind wings are as yet unknown.

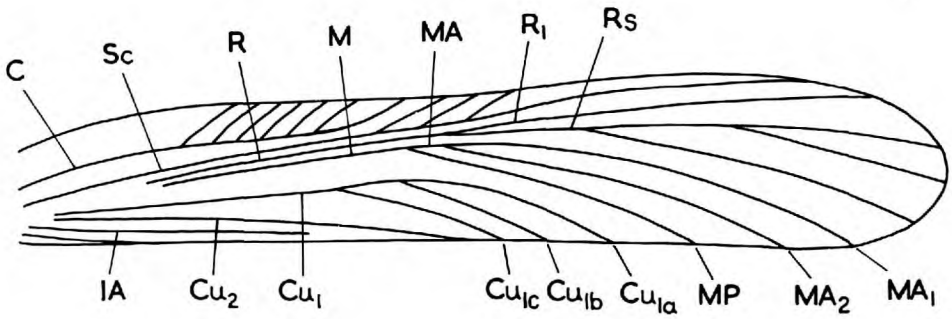


Fig.16. A typical Locustopsid fore wing.

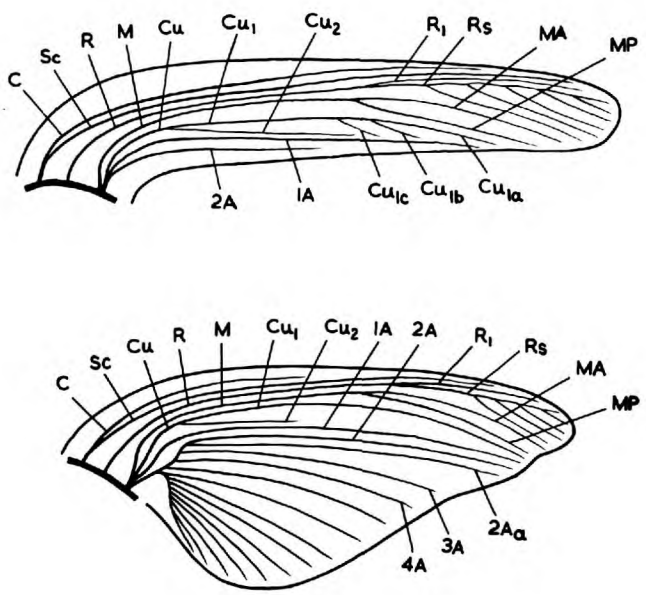


Fig.21. The basic plan of the wing-pad tracheation of Acridid nymphs.

VIII. ACRIDOIDEA - PNEUMORIDAE

1. INTRODUCTION

No more than passing references to Pneumorid wing-venation (see especially Zeuner, 1942) have previously been published. This is rather surprising, as the members of this family have more primitive wings than any of the remaining Acridoidea, and therefore provide an invaluable connecting link with fossil forms.

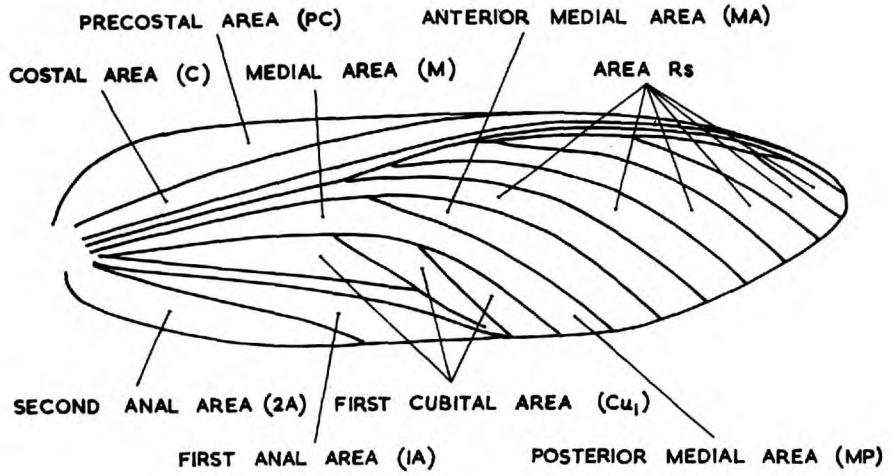
Unfortunately, no nymphs were available, but the tracheation could be seen in the adult wings, and there can be little doubt as to the homologies of the veins.

2. THE SHAPE AND AREAS OF THE WINGS

(a) Fore wing.

As can be seen in Fig. 17, the Pneumorid fore wing is broader that of the Acrididae or Eumastacidae (see figs. 21a and 21b). A lobe may be developed at the base of the anterior margin. The convexities and concavities of the veins of both fore and hind wings are better developed and of a more primitive nature than in other Acridoidea. The anal hinge (a line of weakness developed between Cu_2 and 1A) is not present.

The areas of the wing are similar to those of the more primitive members of the Acrididae; the anal area is however, relatively shorter. The areas are always subdivided into the numerous small cells of the archedictyon.



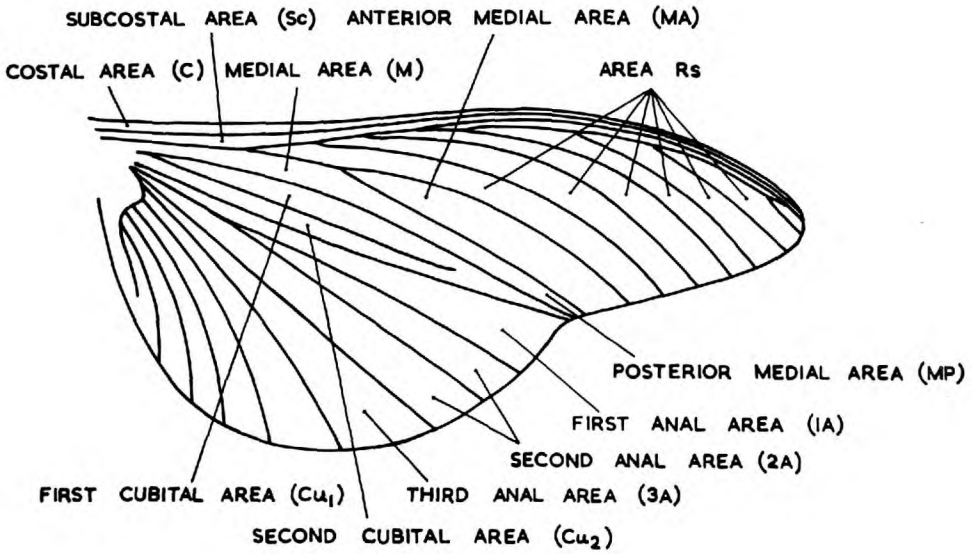


Fig.17. The areas of Pneumorid wings.

(b) Hind wing.

The hind wing is characterized by the anal lobe, though this is relatively smaller than that of most other Acridoidea, being about equal in area to the pre-anal part of the wing. There is an indentation in the wing-margin at the point where the first anal vein reaches it. The names of the areas are given in Fig. 17.

When the wing is at rest the anal lobe is folded up and lies under the pre-anal part of the wing. The folds are formed along the anal veins.

3. THE WING-BASE

No fresh material was available, and the wing-bases of the dried specimens (which could not be treated with potash) were not clear enough for conclusions to be drawn.

4. THE VEINS

The veins of Pneumorid wings (and those of all Orthoptera) may be classified as follows:-

(a) The ambient veins

(b) The longitudinal veins

(i) Primary veins

(ii) Secondary veins

(c) The cross-veins

(d) The archedictyon

The basic plan of the venation of Pneumorid wings is shown in Fig. 18.

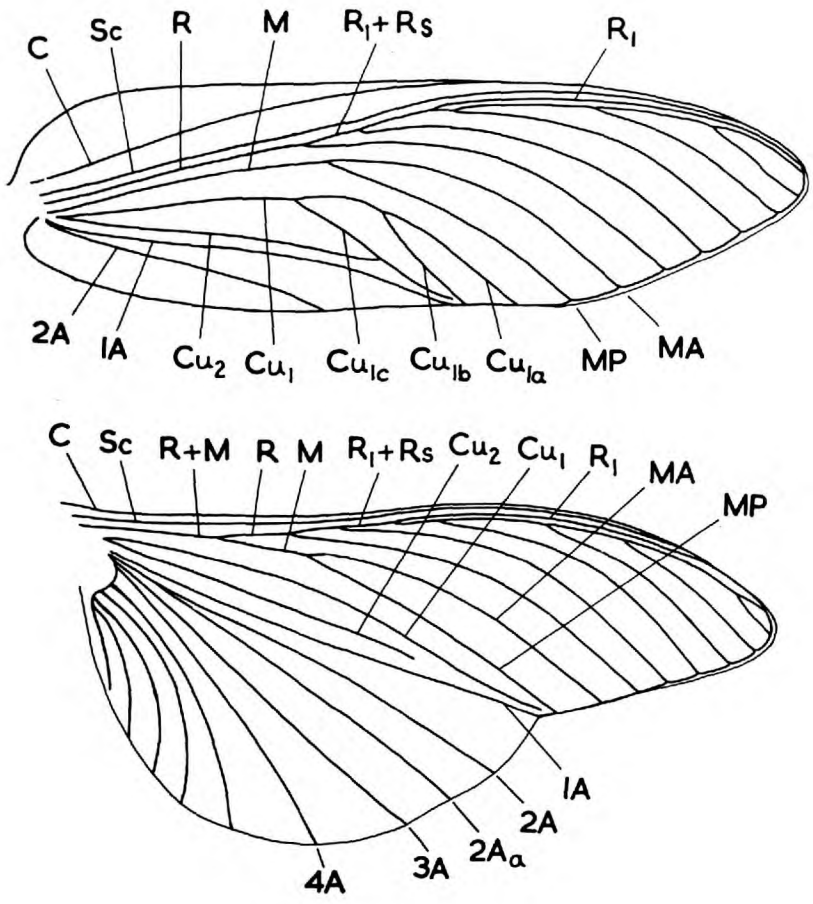


Fig.18. The basic plan of the venation of Pneumorid wings.

(a) The ambient veins.

These are veins developed along or just within the margin of the wing; they are not provided with tracheae, and are differentiated from the archedictyon in the same way as cross-veins. There are two in the fore wing and one in the hind wing.

The first of the ambient veins in the fore wing is developed along the anterior edge of the precostal area, and is here called the anterior ambient vein (AA). It joins the costa distally, where this vein reaches the wing-margin. The other ambient vein of the fore wing runs submarginally from the distal tip of the costa to the base of the wing, towards which it actually forms the posterior wing-margin. It can be divided into the distal ambient vein (DA), running from the tip of the costa to the tip of the first anal vein, and the posterior ambient vein (PA), running from here to the wing-base.

In the hind wing the distal ambient vein is present, and there is also a feebly-developed posterior ambient vein, which, however, becomes obsolete towards the base of the wing.

(b) The longitudinal veins.

(i) Primary veins.

These are the longitudinal veins of the more primitive fossil wings and those of them which have persisted in later forms; their main stems normally have a basal articulation, they are generally preceded by tracheae in the

nymph, and they often bear macrotrichia in the adult. (For a discussion of this definition, see p. 25.)

The primary longitudinal veins will be described individually, beginning in the anterior part of the wing.

THE COSTA (C)

In common with most Saltatoria, the costa of the fore wing lies well below the anterior margin in the proximal half of the wing, reaching it about halfway to the apex.

In the hind wing the costa runs along the whole length of the anterior margin and is convex, a feature only slightly apparent in the fore wing.

The costa is always unbranched.

THE SUBCOSTA (Sc)

This vein runs parallel to the costa and immediately behind it. The space between them (the costal area) is much wider in the fore wing than in the hind wing. The subcosta is concave in both pairs of wings. It is always unbranched.

THE RADIUS (R)

In both pairs of wings the radius runs parallel to, and just behind, the subcosta. In some Bulla species, it becomes divided distally into an anterior, unbranched, R_1, and a posterior, pectinately branched, R_s. In Pneumora, Cystocoelia, Shortridgea, and other Bulla species, however, a certain amount of basal fusion between R_1 and R_s has taken place, with the result that one or two of the R_s branches appear to arise

from the main stem of R, the vein in this region actually being $R_1 + R_s$. ~~This condition, which is identical in the fore and hind wings, is shown in Fig. 19.~~ In Pneumora and Cystocoelia there is generally one R_s branch arising from the fused region, and in Shortridgea usually two.

The main stem of the radius is convex.

THE MEDIA (M)

This vein runs parallel to and a short distance behind the radius. It normally becomes divided into two equally developed branches in both pairs of wings; in the fore wings of Prostalia, however, the media is generally three-branched.

The problem of whether the media is complete, or whether the anterior or posterior media is missing, is difficult to solve in the Acridoidea. The only criterion by which the anterior media can be recognized is its convexity. In primitive wings, each primary longitudinal vein tends to divide into an anterior convex branch and a posterior concave branch (Lameere, 1922, regards the subcosta as a posterior branch of the costa). In the case of the primitively complete media, these branches are the anterior media (MA) and posterior media (MP), respectively (Lameere, op. cit.). In some orders of insects there is reason to believe that the media is only represented by its posterior branch, and the vein is therefore regarded as the posterior media. Palaeolontological evidence

suggests that the posterior media is absent in the Plecoptera and Odonata. The only modern order of insects in which the presence of both branches of the media is fairly certain is the Ephemeroptera, in which the corrugation of the veins is primitive (though probably secondarily accentuated).

In the Acrididae and Eumastacidae, the main stem of the media tends to be concave in the fore wing. In the hind wing it is neutral, lying between the strongly convex R and strongly concave Cu_1. The main stem of the Pneumorid media is concave in the fore wing, and is either neutral or slightly convex in the hind wing.

The fore wing becomes flattened beyond the branching of the media in the former two families, and its branches here can therefore give no indication of its identity. In some Pneumorid fore wings (e.g. some species of Cystocoelia), however, the anterior branch tends to be convex at its base, and the posterior branch concave; this condition is well-marked in some wings and is clearly evidence in favour of the media being complete.

In the hind wings of the Acrididae the anterior branch is concave and the posterior branch convex. This will agree with no interpretation: if the media were complete the opposite would be expected; if it were an anterior media both branches should be convex; and if it were a posterior media they should both be concave. The primitive convexity and

concavity of these branches has evidently been lost. Pneumorid hind wings tend to show a similar condition, though not so well-marked. The Eumastacid media is unbranched in the hind wing.

Fossil evidence in this matter is almost completely lacking. The Acridoid family Locustopsidae has a wing-venation closely resembling that of the Acrididae and Eumastacidae, and the branches of the media, of which there are three, show no definite convexity or concavity. In the Palaeodictyoptera and Protorthoptera the media often shows a clear division into MA and MP. The presence of MA is proved by its convexity in the former order (e.g. Microdictya vaillanti Brongniart - type), but in the Protorthoptera its presence can only be inferred by comparison (though occasionly confirmed by feeble convexity, as in Caloneura subtilis Bolton - type). As discussed on p. 23 et seq., there is a striking resemblance between the Pneumorid fore wing and that of Stenodictya lobata, a Palaeodictyopteran, but the venation of the Protorthoptera (at least to judge by the diagrams of Handlirsch, 1939) is no help in this matter.

The above observations do not form a very sound basis for any conclusions. The only positive evidence is provided by the respective convexity and concavity of the branches of the media in the Pneumorid fore wing, which suggests that these branches are, in fact, MA and MP. It seems therefore reasonable to regard the media of the Acridoidea as complete until any evidence to the contrary becomes available, and this course

has been taken in the present work.

THE CUBITUS (Cu)

The cubitus divides almost at its base into two branches, Cu_1 and Cu_2. In the fore wing these are respectively convex and concave; in the hind wing tendencies in this respect are not so clear, but both branches are inclined to be concave.

Cu_1 and Cu_2 are generally unbranched, but in Cystocoelia Cu_1 is often three-branched. Cu_2 is always less strongly developed than Cu_1, a feature typical of the Acridoidea.

THE ANALS

The fore and hind wings differ markedly in the venation of the anal area, and each will therefore be dealt with separately.

The fore wing.

There are two anals (1A and 2A) in the fore wing. 1A runs parallel to Cu_2, and 2A is a shorter vein just behind it.

The hind wing.

It is impossible to be definite about homologies in the hind wing, owing to the development of the anal lobe (see pp. 28 and 30). The first anal undoubtedly corresponds to 1A in the fore wing, but the names 1A, 2A, etc., are intended to be descriptive rather than suggestive of definite homologies.

1A has a base rather distinct from that of the remaining

anals. Because of this feature, which is usual among Orthopteroid insects, Snodgrass (1935) separates this vein from the other anals as the 'postcubitus' (PCu). As little seems to be gained by the use of this new term (and a lot to be lost in the inevitable, if slight, confusion in terminology which must follow), it has been thought best not to adopt it in the present work, throughout which this vein is therefore referred to as the first anal.

1A runs immediately posterior to Cu_2 as far as the distal ambient vein.

2A and the remaining anals have a common base.

(ii) Secondary veins.

These are longitudinal veins which are not homologous with the longitudinal veins of the more primitive fossil wings. They are of two main types which will be dealt with separately.

A. Intercalary veins.

These are secondary veins with no definite basal attachment, formed from the archedictyon, and very rarely represented by tracheae in the nymph. They are named after the area in which they are developed.

Intercalary veins are not found in Pneumorid fore wings, but they may be developed in the hind wing, between some of the anal veins. They are replaced by accessory veins in the Acrididae and Eumastacidae.

B. Accessory veins.

These are ~~accessory~~ secondary veins arising directly from

primary veins and often preceded by tracheae in the nymph. they are named after the vein from which they arise. (For a more detailed account of the distinction between accessory and primary veins, see p. 26.)

There is only one accessory vein in Pneumorid wings, the second anal accessory ($2A_a$), which arises posteriorly from the base of 2A in the hind wing.

(c) The cross-veins.

These are short, transverse, veins running from one longitudinal vein to another. There are very few in Pneumorid fore wings, but in the hind wings they are well-developped in some regions, notably in areas M and MP.

(d) The archedictyon.

This is a network of non-directional veins. It is a prominent feature of Pneumorid wings, covering the whole of the fore wing, and often a large part of the hind wing.

The archedictyon and cross-veins are simply consecutive stages in wing evolution. In the Acridoidea the formation of cross-veins began at the apex and spread inwards towards the base. Thus the extent of the archedictyon gives a measure of how primitive the wing is. In Pneumorid wings (which are more primitive than those of any other Acridoidea) the archedictyon covers all the fore wing, whereas in the fore wings of the most highly specialized Acrididae it is confined to a very small area at the base of the wing. Forms

such as Oedipoda Audinet-Serville are intermediate.

IX. ACRIDOIDEA - ACRIDIDAE AND EUMASTACIDAE

1. INTRODUCTION

Practically no work has previously been published on Acridid wing-venation. Comstock and Needham (1899, and Comstock, 1918) published a diagram of the wing-tracheation of an Acridid nymph, but did not name the adult wing-veins. Since the work of these authors, Karandikar (1945) has studied the nymphal wing-tracheation of Schistocerca gregaria, but there has been no work on the adult venation of the Acrididae. Attempts have, however, been made to name the veins using the Comstock-Needham System, and as a result the synonymy tabulated in Fig. 20 has arisen.

No more than passing references to the homologies of Eumastacid wing-veins have been previously published (see especially Zeuner, 1942).

2. THE TRACHEATION OF THE NYMPHAL WING-PADS

All the longitudinal tracheae of the wing-pad arise from a transverse basal trachea. The basic plan of the tracheation is shown in Fig. 21.

The costal trachea (C) is generally much shorter than the subcostal trachea (Sc); both are unbranched. The radial trachea (R) is usually divided into R_1 and a pectinate radial sector (R_s). When R_s is present, the R_1 trachea is usually reduced and may be almost absent.

NOMENCLATURE IN THIS WORK	SYMBOL	LUCAS (1920)	HANDLIRSH (1925)	FORBES (1933)	SNODGRASS (1935)	MARTYNOV (1935)	ZEUNER (1939)	KARANDIKAR (1945)	CHOPARD (1949)	BRUNNER (1882)	SAUSSURE (1884)
Anterior ambient vein	AA	Costa									Marginal
Precostal intercalary	IPC										Subcostal
Costa	C	Subcosta	Costa		Costa	Costa	Costa	Costa	Costa	Mediastinal	Mediastinal
Subcosta	Sc		Subcosta		Subcosta	Subcosta	Subcosta	Subcosta	Subcosta	Anterior radial	Humeral
Radius	R	Radius	Radius	Radius	Radius	Radius	Radius	Radius	Radius	Middle radial	Discoidal
Radius-one	R_1		R				R				
Radial sector	R_s		R_s				R_s				
Media	M	Media	Media	Media	Media	Media	Media	Media	Media	Posterior radial	Median
Medial intercalary	IM								Intercalary	Intercalary	Intercalary
Cubitus-one	Cu_1	Cubitus	Cubitus	Cubitus	Cubitus	CuA	CuA	Cubitus	Cu	Anterior ulnar	Anterior ulnar
Branches of cubitus-one	Cu_{1a}						CuA_1				
	Cu_{1b}						CuA_2				
	Cu_{1c}						CuA_3				
Cubitus-two	Cu_2	First anal		Second plical	Postcubitus (PCu)	CuP	CuP	CUS	Cup	Posterior ulnar	Posterior ulnar
First anal	1A	Second anal		Third plical	First vannal	Anal		First anal	Anal	Vena dividens	Anal
Second anal	2A	Third anal		Axillary	Second vannal	Axillary		Second anal	Axillary	Vena plicata	Axillary
Posterior ambient vein	PA				Third vannal						Sutural

(a) Fore wing

Fig. 20. Comparative table showing the nomenclatures used by various authors for Acridid wing-veins.

NOMENCLATURE IN THIS WORK	SYMBOL	LUCAS (1920)	HANDLIRSCH (1925)	FORBES (1933)	SNODGRASS (1935)	MARTYNOV (1935)	KARANDIKAR (1945)	CHOPARD (1949)	BRUNNER (1882)	SAUSSURE (1884)
Costa	C	Subcosta	Costa	Costa	Costa	Costa	Costa	Costa		Mediastinal
Subcosta	Sc		Subcosta	Subcosta	Subcosta	Subcosta	Subcosta	Subcosta	Mediastinal	Humeral
Radius	R	Radius	Radius	Radius	Radius	Radius	Radius	Radius	Radial	Discoidal
Radius-one	R_1		R	R_1	R_1					
Radial sector	R_s		R_s	R_s	R_s					
Media	M	Media		Media	Media	Media	Media	Media		Median
Cubitus-one	Cu_1	Cubitus		Cubitus	Cubitus	CuA	CU_1	Cu	Anterior ulnar	Anterior ulnar
Cubitus-two	Cu_2	First anal		First plical	Postcubitus (PCu)	CuP	CU_2	Cup	Posterior ulnar	Posterior ulnar
First anal	1A	Vena dividens		Second plical	Vena dividens	1A	A_1	Anal	Vena dividens	Anal
Second anal	2A			Third plical	First vannal	$2A_1$	A_2	Axillaries		Anterior axillary
Second anal accessory	$2A_a$			Axillary	Second vannal	$2A_2$	A_3			Posterior axillary / False radiate
Third anal	3A					First jugal	A_4			First radiate

(b) Hind wing

Fig. 20. Comparative table showing the nomenclatures used by various authors for Acridid wing-veins (contd.).

The medial trachea (M) is typically bifurcate in the Acrididae, but may be unbranched in wings with reduced venation. In the Eumastacidae the medial trachea is normally bifurcate in the fore wing and unbranched in the hind wing.

The cubital trachea (Cu) of the fore wing-pad is divided near its base into two branches (Cu_1 and Cu_2) in the Catantopinae, in Lamarckiana of the Pamphaginae, and in Chorotypus of the Eumastacidae. The Cu_1 trachea is not usually present in the Acridinae or Oedipodinae, and it is doubtful if it occurs in the Pyrgomorphinae. It seems likely that it is usually developed in the Eumastacidae. Where it occurs in Acridid fore wing-pads, it is generally also present in the hind wing-pads, though always reduced. It is not known whether it is present in Eumastacid hind wing-pads.

A three-branched Cu_1 trachea is typical of many Acridid fore wing-pads, but the Eumastacidae and the Acridid subfamily Ommexechinae have an unbranched Cu_1. The Cu_1 trachea is normally unbranched in the hind wing-pad.

There are two anal tracheae (1A and 2A) in the fore wing-pad; in the hind wing-pad the number of anal tracheae depends on its size (there are rarely more than six). The first anal trachea of the hind wing-pad arises separately from the remainder.

From a study of nymphs which were approaching the final moult, and thus showing the adult venation superimposed on the tracheae, it is clear that the adult veins follow exactly

the courses of the nymphal tracheae.

3. THE VENATION OF THE ADULT WINGS

The following subfamilies of Eumastacidae are always apterous or microalate:-

Morabinae	Mastacideinae
Tanaeocerotinae	Episactinae
Teicophryinae	Malagassinae
Gomphomastacinae	Miraculinae
Morseinae	

(a) The areas.

No attempt has been made in the past to give names based on the Comstock-Needham System to the areas of Acridid and Eumastacid wings. A proposed scheme is shown in Fig. 21. Each area (except the precostal area) is named after the vein which forms its anterior boundary.

The areas are always subdivided into cells.

The precostal area (PC), which only occurs in the fore wing, is often produced anteriorly to form a precostal lobe.

(b) Folding.

The flexed fore wing is generally folded perpendicularly along the anal hinge, which lies between Cu_2 and 1A. This enables the anal area to be horizontal while the remainder of the wing is in a vertical position, this being suitable

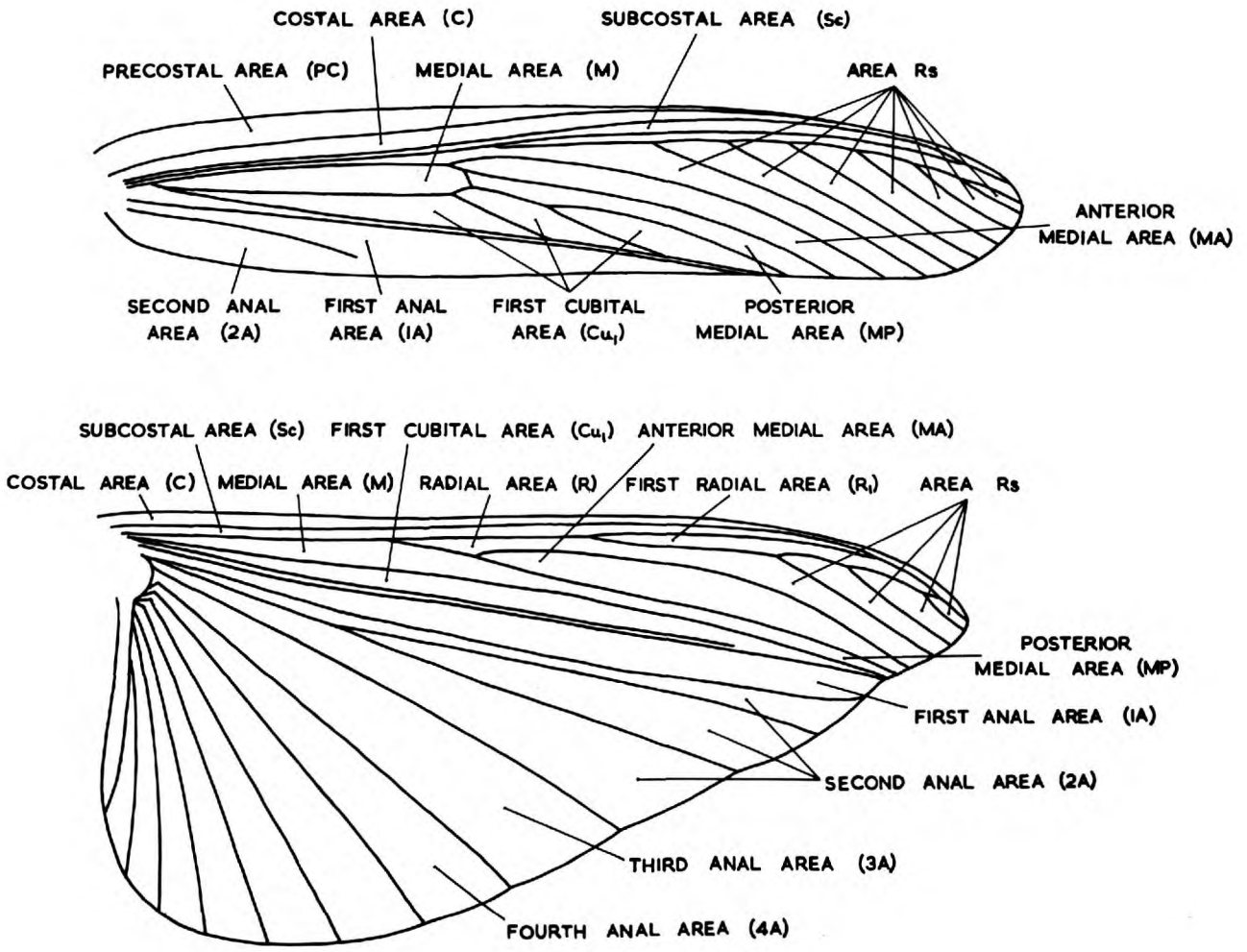
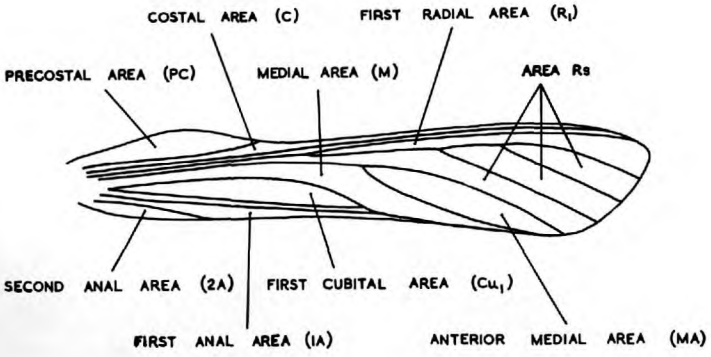


Fig.21a. The areas of Acridid wings.



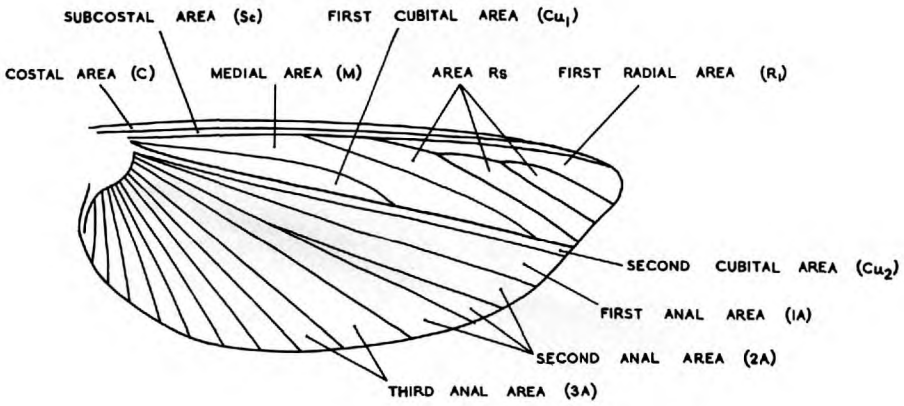


Fig.21b. The areas of Eumastacid wings.

for femoro-alary stridulation. The folding of the hind wing, when at rest, is more complicated, due to the presence of the large anal area. The most anterior fold lies along or just behind Cu_2; the remainder lie along $2A_a$, 3A, $4A_a$, 4A, $5A_a$, etc.

(c) The wing-base.

At the base of each wing there is a flexible region which allows the wing to be extended or flexed. Between the bases of the wing-veins and the thoracic terga, is the axillary membrane, softer and more flexible than the wing-membrane. In the axillary membrane, each wing typically has two median plates and four axillary sclerites articulating with the bases of the veins and the thoracic tergum.

Snodgrass (1929) has described and illustrated the wing-bases of Dissosteira carolina Linnaeus, a member of the Oedipodinae. More recently, La Greca (1947) has published a wider study, embracing representative species from the subfamilies Acridinae, Oedipodinae, Catantopinae, Pyrgomorphinae, and Pamphaginae. He gives diagrams of the wing-bases of Anacridium aegyptium (Linnaeus). The wing-bases of Locusta migratoria Linnaeus are illustrated in Fig. 22; they are very similar to those of Dissosteira and Anacridium.

The base of each wing is dealt with separately below.

Fore wing.

The first axillary sclerite is situated between the mesonotum and the second axillary. It has an anterior process

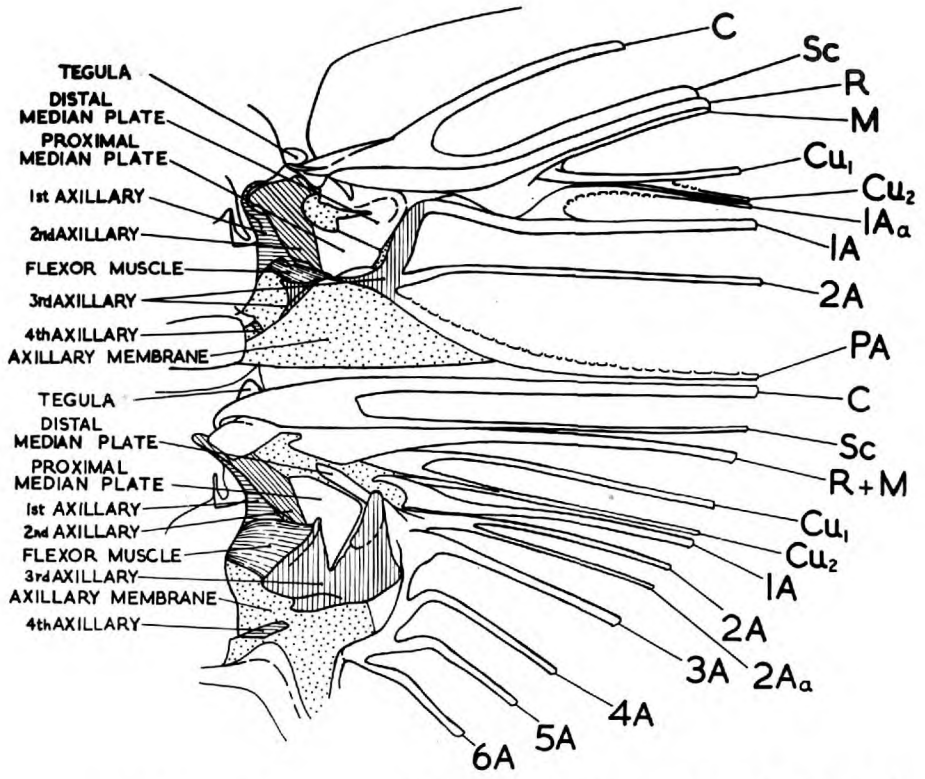


Fig.22. The wing-bases of Locusta migratoria.

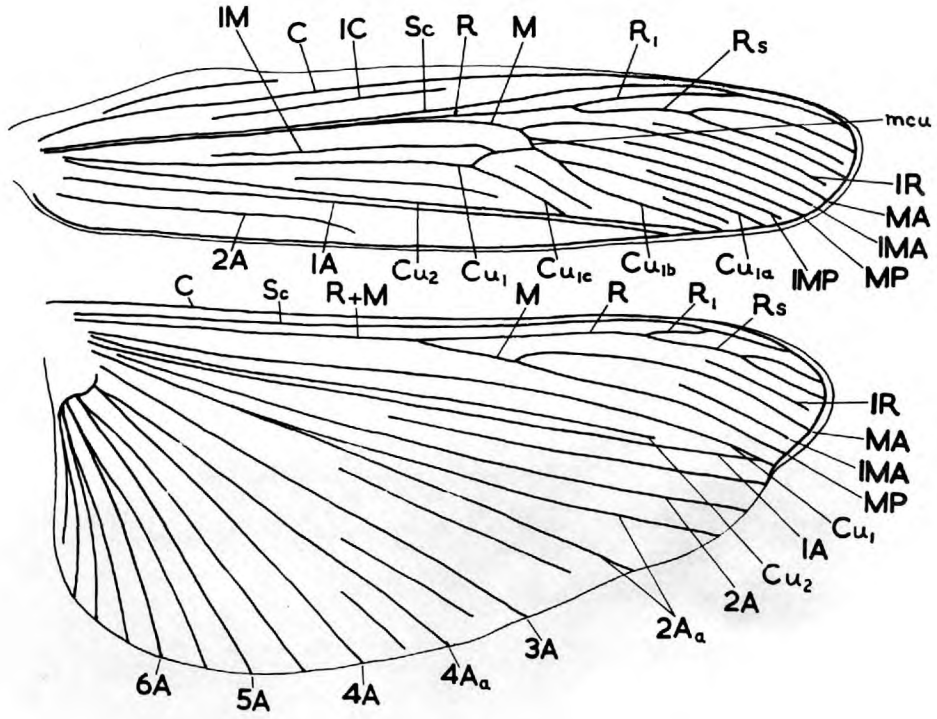


Fig.25b. The wings of Mecostethus grossus, female.

which articulates with the fused bases of the costa and subcosta. Near the base of the former vein there is a tegula.

The second axillary articulates anteriorly with the base of the radius, and posteriorly with the proximal median plate. The distal median plate also intermediates between the base of the radius and the proximal median plate, but is distal to the second axillary, there being a small area of axillary membrane between the two. The base of the media articulates with the distal median plate. The base of the cubitus arises from the media a short distance from this articulation.

Ivanova (1947) has shown that the second axillary in Calliptamus italicus Linnaeus and other unspecified insects has a dual origin embryologically. She therefore regards this sclerite as consisting of a dorsal component, the second axillary proper, and a ventral component which she has named the 'pleural axillary'.

The anal veins and the posterior ambient vein arise from the third axillary, which articulates with the posterior part of the mesonotum via the fourth axillary. The latter is a small sclerite more closely connected with the third axillary in Dissosteira than in Locusta or Anacridium. The third axillary is also connected with the proximal and (to a less extent) distal median plates. Inserted on it is the flexor muscle of the wing.

The first and fourth axillaries are confined to the

dorsal surface of the axillary membrane, whereas the second and third axillaries are exposed on both dorsal and ventral surfaces.

The base of Cu_2 is much less definite than the bases of the other primary veins. Posterior and proximal to the base of this vein is the base of the first anal accessory (see p. 82). The base of the anal fold lies between this secondary vein and the base of the cubitus.

When the wing is flexed a fold occurs between the median plates.

Hind wing.

The axillary sclerites of the hind wing are basically similar to those of the fore wing.

The first axillary has a reduced anterior process which does not reach the fused bases of the costa and subcosta. As in the fore wing, there is a tegula at the base of the costa.

The second axillary and the median plates are similar to those of the fore wing. The distal median plate, however, is considerably reduced. The base of the media is completely fused with the radius, but an articulation with the distal median plate is retained. The cubitus arises from the base of the media as in the fore wing.

The first anal vein of the hind wing has no direct connection with an axillary sclerite, and has a base distinct

from those of the remaining anals. The latter are all joined together at the base, and are connected anteriorly with the third axillary; this sclerite provides a large insertion for the flexor muscle of the hind wing. As in the fore wing, the third axillary is connected with each of the median plates. It articulates with the metanotum via a small fourth axillary.

In the species examined, Cu_2 has a double origin in the hind wing. The anterior part arises from Cu_1, and the posterior part from 1A; the two parts join immediately. The constituent arising from 1A should strictly be termed the first anal accessory ($1A_a$), thus making the complete vein Cu_2+ 1A. As a definite interpretation of this feebly-developed structure is at present impossible, it has been thought best to refer to the complete vein (for the time being) as Cu_2. The base of this vein is also the base of the first (concave) anal fold, as the two lie approximately on the same line.

The base of the second (convex) anal fold (which runs just posterior to 1A) lies between the bases of 1A and 2A. The third (concave) anal fold lies along $2A_a$ and its posterior branch. The remaining anal folds, which are alternately convex and concave, lie along 3A (convex), $4A_a$ (concave), etc.

(d) The veins.

The veins of Acridid and Eumastacid wings may be classified in the same way as those of the Pneumoridae, and the various types are defined under ~~this~~ that family (see p. 66 et seq.).

The typical venation of Acridid and Eumastacid wings is illustrated in Figs. 23a&b and 24.

(i) The ambient veins.

In the fore wing there is an anterior ambient vein (AA) developed along the leading edge as far as the point where the costa (or precostal intercalary) joins the latter. There is also an ambient vein running from the distal end of the costa to the base of the wing; this vein may be divided into the distal ambient vein (DA) and the posterior ambient vein (PA).

In the hind wing the distal ambient vein is always developed, and in the Eumastacidae there is almost always a posterior ambient vein in addition to this.

(ii) The longitudinal veins.

A. Primary veins.

The nature of these veins is very similar throughout the Eumastacidae and less specialized Acrididae.

THE COSTA (C)

In the fore wing the origin of the costa lies well behind the anterior margin; it usually reaches the latter from a third to two-thirds of the way along it.

In the hind wing the costa runs along the whole length of the anterior margin and is strongly convex, a feature not shown by the fore wing.

The costa is always unbranched.

THE SUBCOSTA (Sc)

This vein runs parallel to the costa and immediately

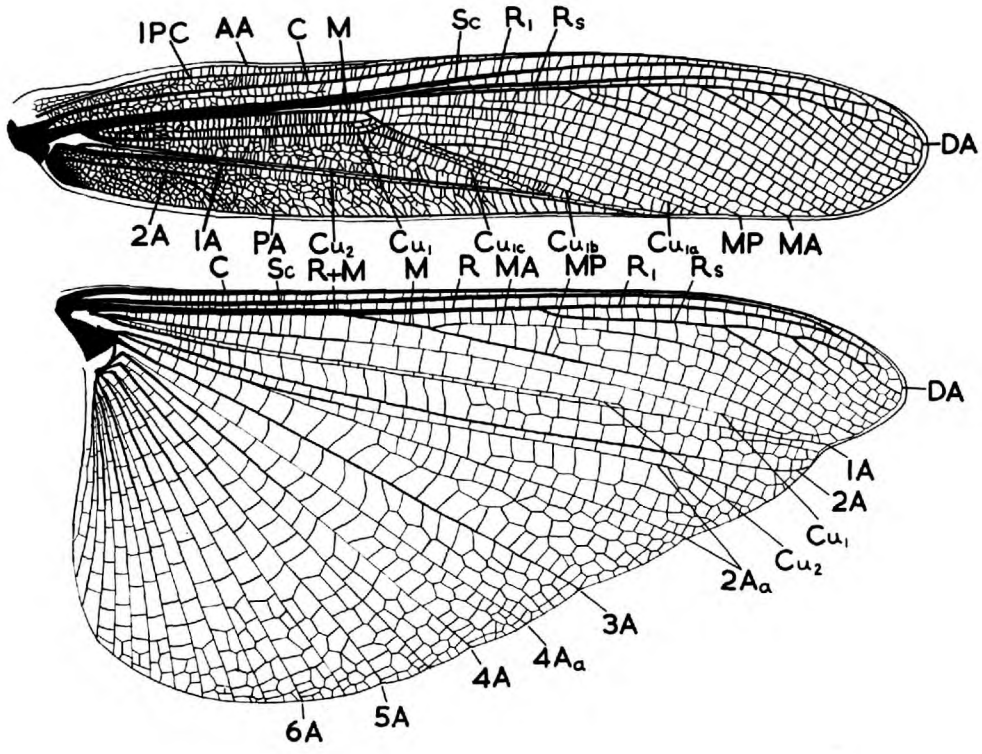


Fig.23a. The wings of Locusta migratoria.

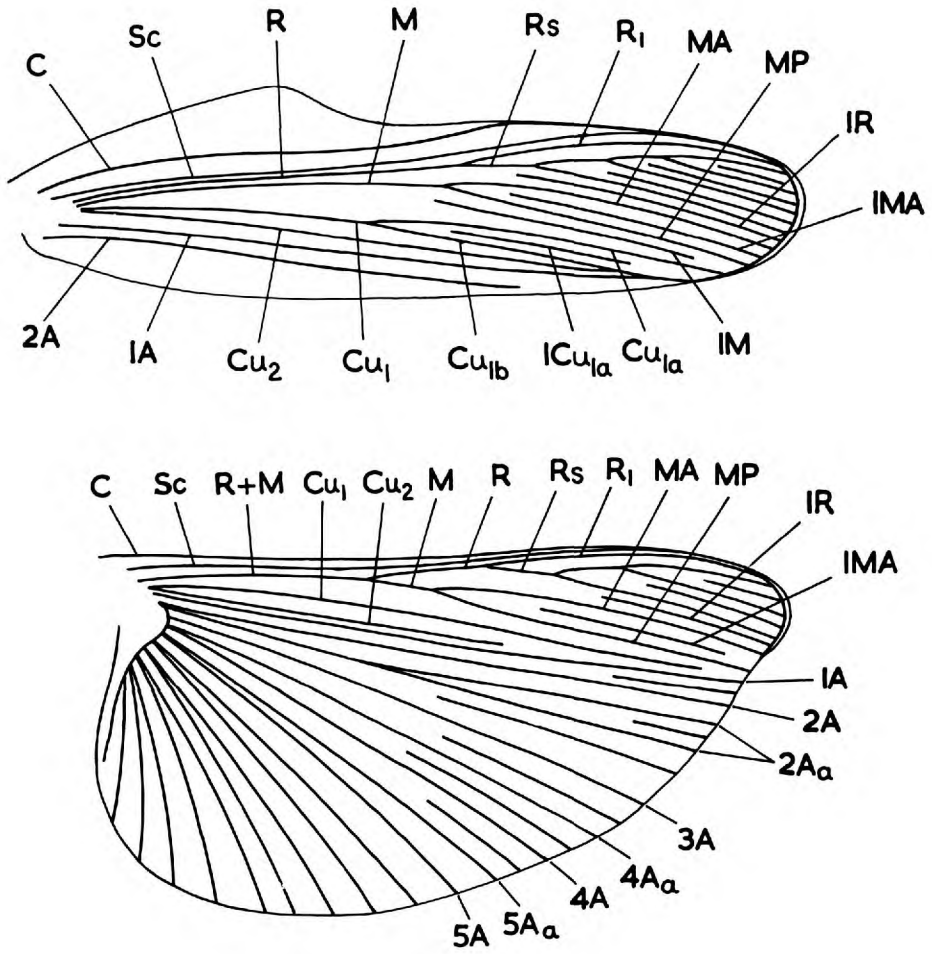
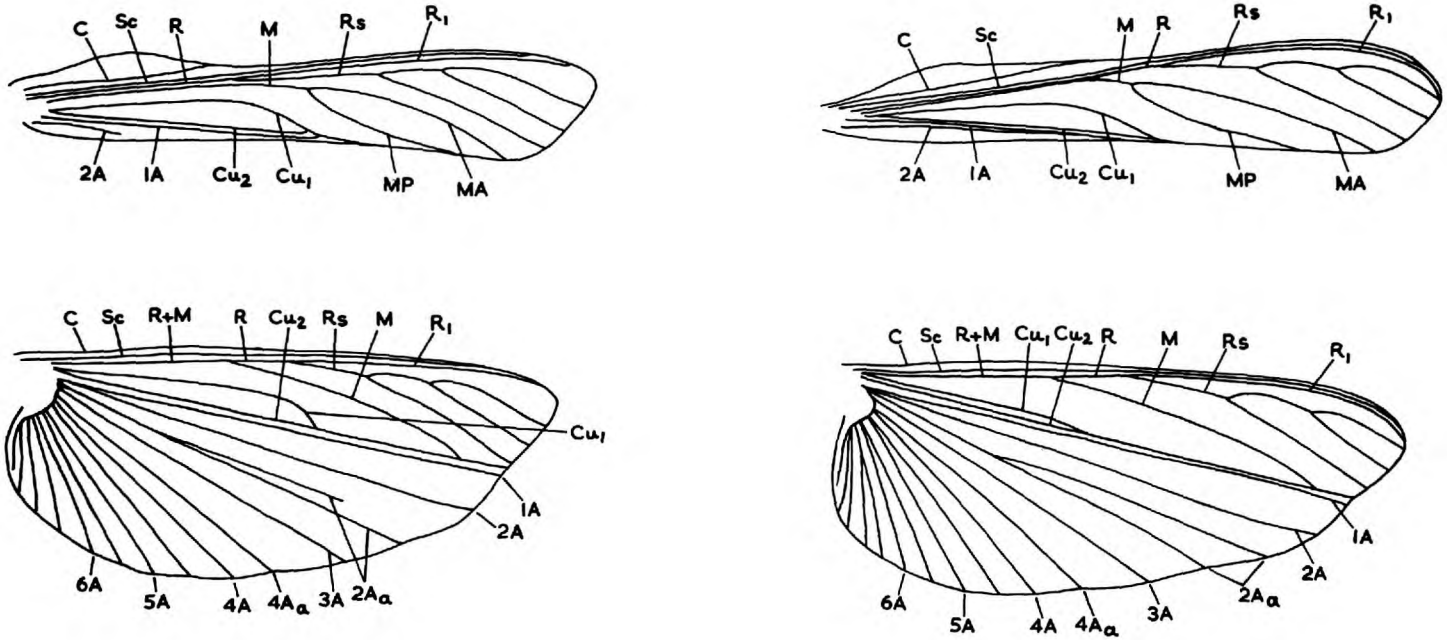


Fig.23b. The wings of Poecilocerus.



Erianthus

Erucius

Fig.24. The typical venation of Eumastacid wings.

behind it. At its termination, it either joins C, R_1, or DA.

In the Acridid fore wing the subcosta becomes concave after separating from the convex radius. The subcosta of the less specialized fore wings of the Eumastacidae is concave throughout its length, as it is in the hind wings of both families.

THE RADIUS (R)

The radius runs parallel to and just behind the subcosta; its base is closely applied to this vein in the fore wing, though remaining completely separate in the hind wing.

In typical Acridid and Eumastacid wings, the radius becomes divided in the distal part of the wing into an anterior single branch (R_1) and a pectinately divided posterior branch (R_s). In the Acridinae the venation is usually reduced and the radius may be unbranched (especially in the hind wing), but there is usually a small sector, which is often simple (e.g. Myrmeleotettix maculatus (Thunberg), Fig. 24b) or merely bifurcate (e.g. Omocestus viridulus (Linnaeus), Fig. 24a). In the Trigonopteryginae the main stem of R_s has secondarily fused with R_1, so that the branches of R_s appear to arise directly from the radial stem.

The number of branches to the radial sector often varies in different individuals of the same species, and may in fact do so on different sides of the same individual. The table given in Fig. 25 shows the type of variation found in the number of R_s branches in Locusta migratoria. It also shows an apparently inexplicable inverse correlation between the number

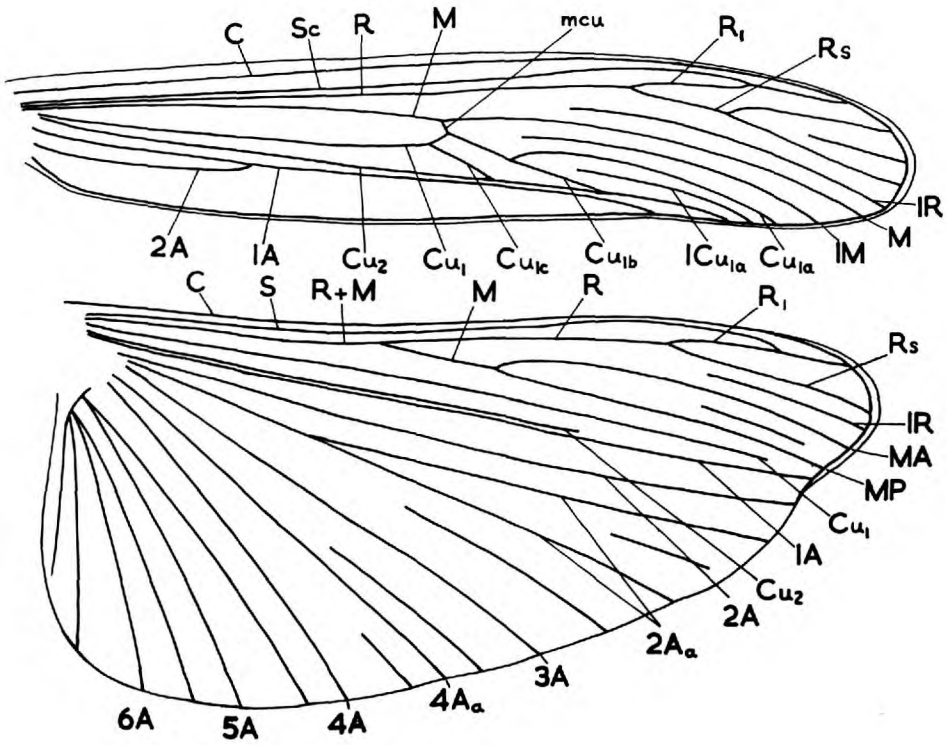


Fig.24a. The wings of Omocestus viridulus, female.

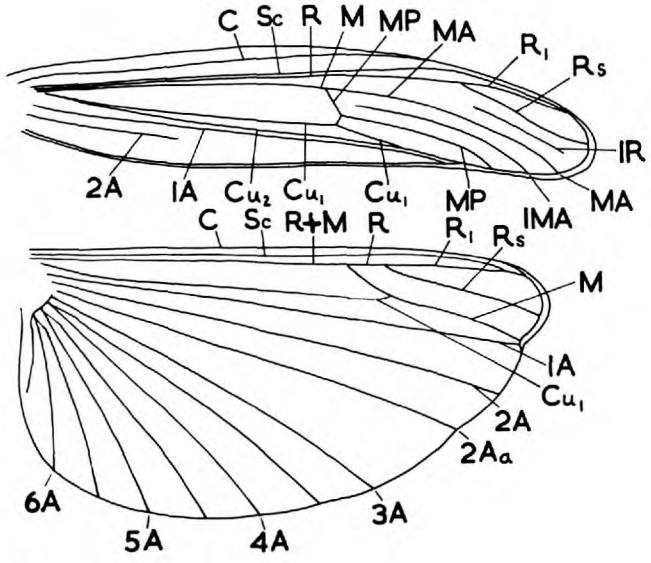


Fig.24b. The wings of Myrmeleotettix maculatus, female.

SIDE	MALE			FEMALE		
	WING LENGTH (m.m.)	NUMBER OF R_s BRANCHES		WING LENGTH (m.m.)	NUMBER OF R_s BRANCHES	
		FORE WING	HIND WING		FORE WING	HIND WING
LEFT	40	7	3	44	8	4
RIGHT		6	3		7	4
LEFT	40	7	3	45	7	4
RIGHT		6	3		8	3
LEFT	41	7	4	45	6	4
RIGHT		7	4		7	3
LEFT	41	7	4	46	8	5
RIGHT		6	4		8	4
LEFT	44	5	3	46	8	4
RIGHT		7	4		8	4
LEFT	45	6	4	50	7	4
RIGHT		6	3		7	3
LEFT	45	6	3	51	6	3
RIGHT		6	3		6	4
LEFT	45	6	3	51	6	3
RIGHT		6	3		6	3
LEFT	47	6	3	52	6	4
RIGHT		6	4		6	3
LEFT	48	6	4	52	6	3
RIGHT		6	3		6	3

Fig.25. Table showing the variation in the number of Rs branches in the wings of Locusta migratoria.

of R_s branches and the length of the wing.

THE MEDIA (M)

The base of this vein is closely applied to the radius in most Acridid fore wings; in the Eumastacidae and the Acridid subfamily Charilainae (e.g. Charilaus), however, it is often rather more separate. In the fore wings of Systella (Fig.25a) and Trigonopteryx the media is fused for part of its length to the radius. This condition is also found in the males of Mecostethus grossus (Linnaeus) (Fig.25b); in the females of this species the fusion is less well-marked.

In the hind wing the base of the media is always fused to the radius. The point of separation is usually in the proximal half of the wing, but may be in the distal half in more specialized wings (e.g. Myrmeleotettix maculatus).

Shortly after leaving the radius, the media is typically divided into two equally developed branches (MA and MP) in the fore wing. In the Acrididae this is equally true of the hind wing, but the media is unbranched in Eumastacid hind wings. In the more specialized wings of the Acridinae the media ~~is~~ may be undivided in the fore wing (e.g. Omocestus viridulus), or in the hind wing (e.g. Myrmeleotettix maculatus), or even in both pairs of wings (e.g. Chorthippus parallelus (Zetterstedt) (Fig. 25c, d). In the fore wings of Paulinia MA is fused to the radius for part of its length. The media is rarely three-branched (e.g. Aphantotropis; Parossa bimaculata (Giglio-Tos), fore wing (Fig.25e).

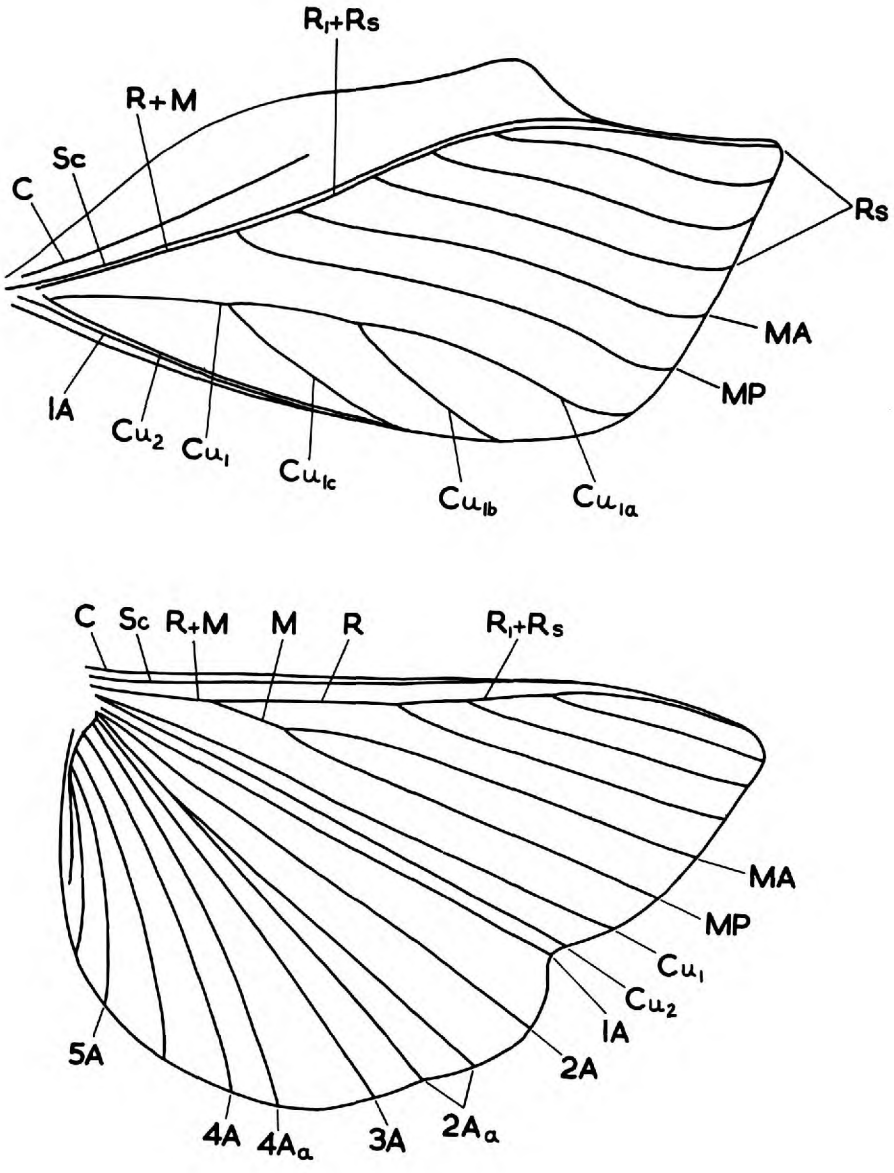


Fig.25a. The wings of Systella.

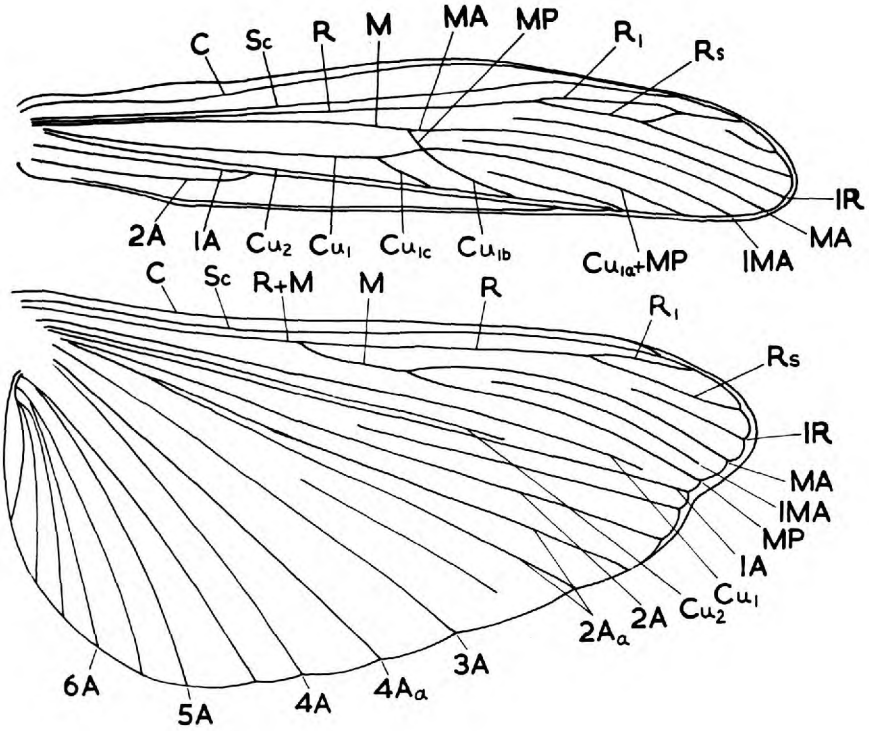


Fig.25i. The wings of Chorthippus bicolor, male.

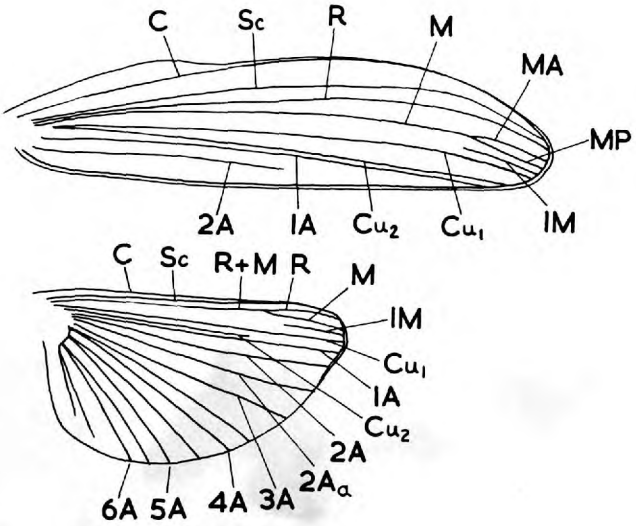


Fig.25c. The wings of Chorthippus parallelus, male (slightly macropterous).

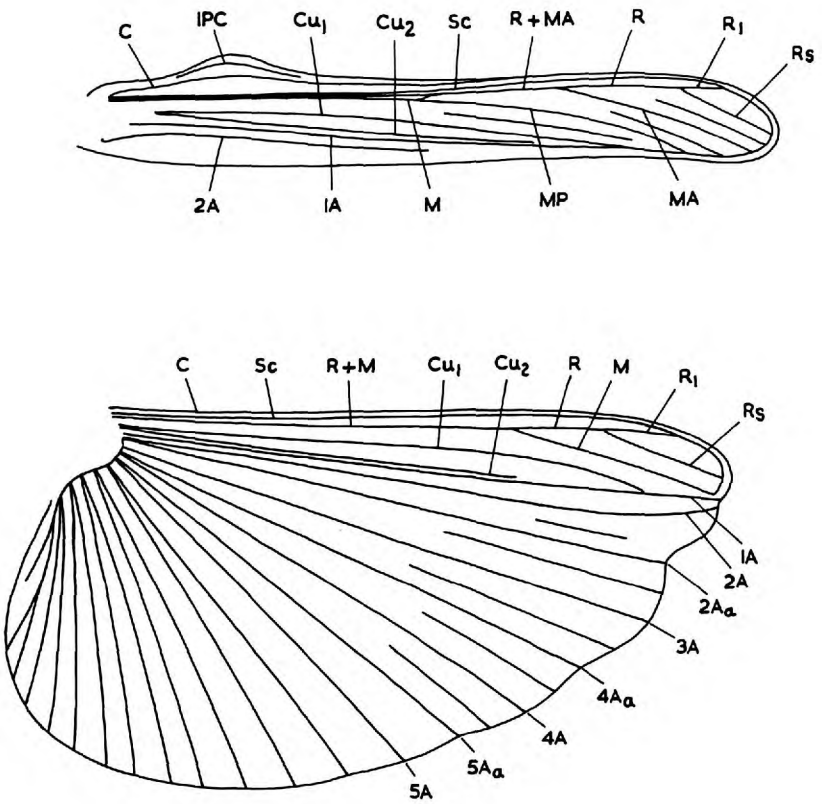


Fig.25d. The wings of Paulinia.

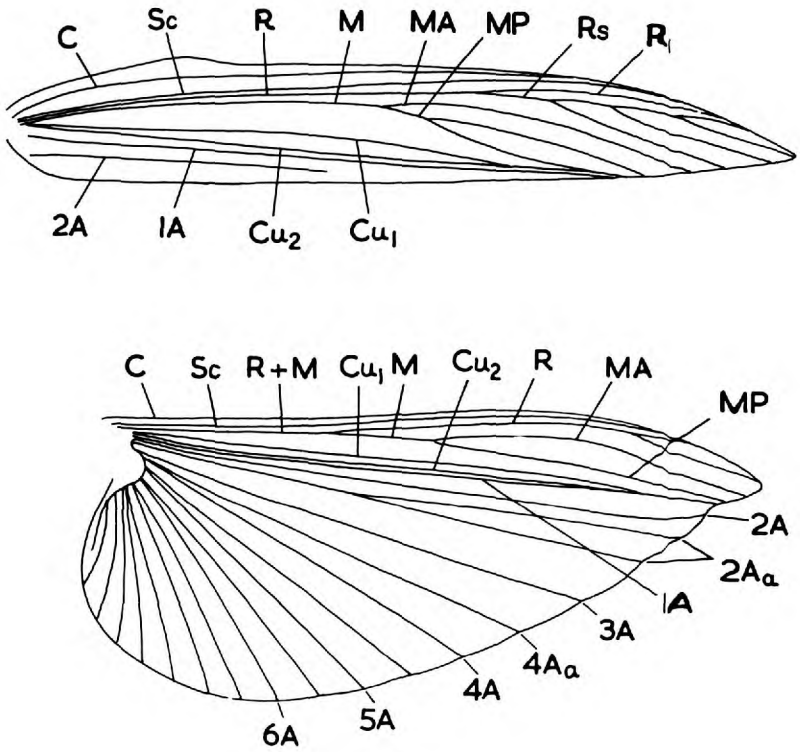


Fig.25e. The wings of Parossa bimaculata.

The application of the terms MA and MP to the medial branches is discussed under the Pneumoridae (p. 69 *et seq.*).

THE CUBITUS (Cu)

The cubitus arises from the base of the media in the fore wing, and from the common base of the media and radius in the hind wing. Close to its origin it divides into two branches (Cu_1 and Cu_2) in both pairs of wings. In each case Cu_1 is developed more strongly than Cu_2, especially in the Acrididae. It is clear that one of the features of the Acridid line of evolution has been the suppression of Cu_2.

In the Acridid fore wing Cu_1 is typically bifurcate distally at about the some level as the bifurcation of the media, and the anterior branch usually divides again in the Catantopinae, Oedipodinae, and Acridinae. In the Ommexechinae and Eumastacidae, however, Cu_1 is unbranched, and is sometimes so in the Pyrgomorphinae. Cu_1 rarely has more than three branches in the fore wing; an example of this is *Choroedocus*, in which it is four-branched in many cases.

The three typical branches of Cu_1 are referred to in this work as Cu_{1a}, Cu_{1b}, and Cu_{1c}, beginning anteriorly.

In the hind wing Cu_1 is almost always unbranched, running in a straight line to the wing-margin. It tends to be two-branched, however, in the larger species of *Lamarckiana*.

Cu_2 is always straight and unbranched in both pairs of wings. In the fore wing it lies directly anterior to the

anal fold and probably functions as a support for this line of weakness. In the hind wing Cu_2 lies more or less in the first anal fold and is generally degenerate, not reaching the distal ambient vein. In reduced hind wings Cu_2 may be absent.

Cu_1 may be convex or concave in the fore wing; it is always concave in the hind wing. Cu_2 shows no tendency in this respect in the fore wing, but in the hind wing it is rather concave (lying in the first anal fold).

It should be pointed out here that from a study of the Acrididae and Eumastacidae alone it would be quite feasible to regard Cu_2 as a secondary vein and Cu_1 as the complete cubitus. Its weak development (compared with Cu_1) and the lack of the Cu_2 trachea in many nymphs would support this view. Also, the strong concavity of Cu_2 in the hind wing would fit in better with it being the complete cubitus. In the Pneumoridae, however, Cu_1 and Cu_2 are convex and concave, respectively, in the fore wing; in the hind wing Cu_1 is rather concave. As the correspondence between these veins is quite clear, convexity and concavity cannot be relied upon in these families, as was found with the media.

It is not difficult to find a possible explanation for the present convexities and concavities, if one assumes that mechanical factors require the primary veins to be alternately convex and concave, and that when during evolution two veins become closely approximated they are functionally equivalent to

one. (It should be realised that the account given below is a hypothesis and is only put forward as a tentative suggestion.) In a Palaeodictyopteran such as Stenodictya (and it seems probable that an insect of this type was ancestral to the Pneumorid - Locustopsid - Eumastacid - Acridid line of evolution) the media divides at the same level as the division of the radius into R_1 and R_s. MA is convex because it comes immediately posterior to the concave radial sector, which in turn follows the convex R_1; the latter is well separated from the main stem of R_s. In the Acridid line the stem of the radial sector moved towards R_1. It could thus remain concave no longer and became convex alongside R_1. This convexity was not very strong, as in the same process R_1 lost some convexity to R_s. In order to fit in with the increased convexity of R_s, MA had to become less convex and finally became concave - the condition found in most Acrididae. This process probably began at the base of MA, and , as the distal half of the wing became flattened, there was no need for the convexity of this vein to spread to the wing-margin. MP then became convex and Cu_1 concave, as the process spread posteriorly. The Pneumorid fore wing shows an intermediate stage: MA has lost its convexity, but Cu_1 still retains it.

In the hind wing a similar process occurred. In this case, however, it was accelerated by the moving outwards of the origin of R_s and the migration of the division of the towards the wing-base. This brought the origin of MA into a

position immediately behind the strongly convex main stem of the radius, and thus it became concave. MP became convex and Cu_1 concave, as in the fore wing. This is well illustrated in the Pneumoridae, and there is a slight tendency for Cu_2 to become convex near the base. In the Acrididae any convexity which may have been acquired by Cu_2 in the hind wing has been obscured by the occupation by this vein of the first anal fold.

In most Pneumorids the base of the stem of R_s has actually fused with R_1, so that the basal branches of R_s arise from what appears to be the main stem of the radius, but is in fact $R_1 + R_s$. (These basal branches of Rs are regarded by Zeuner (1942) as a detached part of the media, which he therefore considers is a specialized vein in the Pneumoridae.) R_1 and the main stem of R_s are completely fused together in the Acridid subfamily Trigonopteryginae.

From the above account it is clear that the Acridoidea illustrate well the limitations to using convexity and concavity as criteria in identifying wing-veins. The Cu_2 trachea in the Pneumoridae and many of the Acrididae and Eumastacidae confirms the view that it is a primary vein.

THE ANALS

Fore wing.

There are almost always two anals (1A and 2A) in the fore wing. 1A runs just posterior to Cu_2 for the whole of its length, terminating at the ambient vein. It gives rise to

the first anal accessory vein (which supports the posterior side of the anal hinge) near its base.

2A is a shorter vein, generally less than half the length of 1A. It is sometimes very feebly developed (e.g. Erianthus versicolor Brunner, Fig. 24).

Hind wing.

As under the Pneumoridae (see p. 72). 4A and all the anals posterior to it each have an accessory vein arising anteriorly from their bases; these accessory veins form the concave ribs of the anal fan, the convex ribs of which are formed by the anal veins themselves.

B. Secondary veins.

Intercalary veins.

The Eumastacidae never have well-defined intercalary veins. Those of the Acrididae will be treated in turn, beginning anteriorly.

Fore wing.

PRECOSTAL AREA

In the Acridinae and Oedipodinae there is often a precostal intercalary (IPC) between AA and C.

COSTAL AREA

There is sometimes a costal intercalary (IC) between C and Sc in the more specialized wings.

RADIAL AREA

There are nearly always intercalary veins between the

branches of R_s and between R and MA.

MEDIAL AREA

There is almost always an intercalary vein (IMA) between the branches of M, and generally another (IMP) between MP and Cu_1.

There may be a medial intercalary (IM) between the main stem of the media and the main stem of Cu_1. This is characteristic of the Oedipodinae, in which it is equipped with pegs for stridulation. Mecostethus is similar in this respect. A medial intercalary (without pegs) is occasionally found in other forms (e.g. some species of Euprepocnemis). Where it is used as a stridulatory rib IM is strongly convex.

CUBITAL AREA

There is usually an intercalary (ICu_{1a}) between Cu_{1a} and Cu_{1b}; there is also another (ICu_{1b}) in some Acridid wings between Cu_{1b} and Culc. There may be one (ICu_1) between the main stem of Cu_1 and Cu_2.

ANAL AREA

Occasionally this area has an intercalary.

Hind wing.

RADIAL AREA

When the branches of the radial sector are well-developed, there are nearly always intercalaries between them. There is usually another (IR) between R and MA.

MEDIAL AREA

An anterior medial intercalary (IMA) is usually developed.

ANAL AREA

In the larger forms there are frequently intercalaries between the primary anal veins and their accessory branches.

Accessory veins.

These will be described in turn, beginning anteriorly.

Fore wing.

THE FIRST ANAL ACCESSORY ($1A_a$)

This is a straight vein lying just posterior to the anal hinge. It arises anteriorly from the base of 1A, and follows the anal fold for most of its length.

Hind wing.

THE FIRST ANAL ACCESSORY ($1A_a$)

See p. 82.

THE SECOND ANAL ACCESSORY ($2A_a$)

This arises posteriorly from the base of 2A. It almost always divides into two branches in the proximal half of the wing, the anterior one of which is always the more strongly developed. Rarely 2A is unbranched.

THE FOURTH AND REMAINING ANAL ACCESSORIES ($4A_a$, $5A_a$, etc.)

Practically all the anal veins from 4A onwards have accessory veins, one arising anteriorly from the base of each.

(iii) The cross-veins.

The only cross-vein which requires special attention is that connecting M or MP to Cu_{1a+b} in the Acridid

fore wing, near the bifurcation of M, thus closing the medial area. This cross-vein is often more strongly developed than the others, sometimes having the appearance of a longitudinal vein. When it is absent the medial area is either open (e.g. the Eumastacidae; Lamarckiana, Fig. 25f; Teratodes, Fig. 25h) or closed by the branches of M and Cu (e.g. Chorthippus bicolor (Charpentier), Fig. 25i). This medio-cubital cross-vein is here given the symbol mcu, when strongly developed, though this name could apply to any cross-vein connecting M and Cu.

(iv) The archedictyon.

The relation between the archedictyon and the cross-veins is discussed under the Pneumoridae (p. 74).

In the more primitive fore wings (e.g. Lamarckiana; Teratodes; Chorotypus, Fig. 25j) the archedictyon covers practically the whole of the area of the wing; in the most specialized forms, however, there are a very few small areas of archedictyon in the basal and posterior parts of the wing (e.g. most of the Acridinae; Erianthus). Many of the Oedipodinae (e.g. Oedipoda coerulescens (Linnaeus)) show an intermediate stage.

The hind wing is almost invariably devoid of archedictyon; one exception to this is Lamarckiana, which has a small distal area of archedictyon in the hind wing.

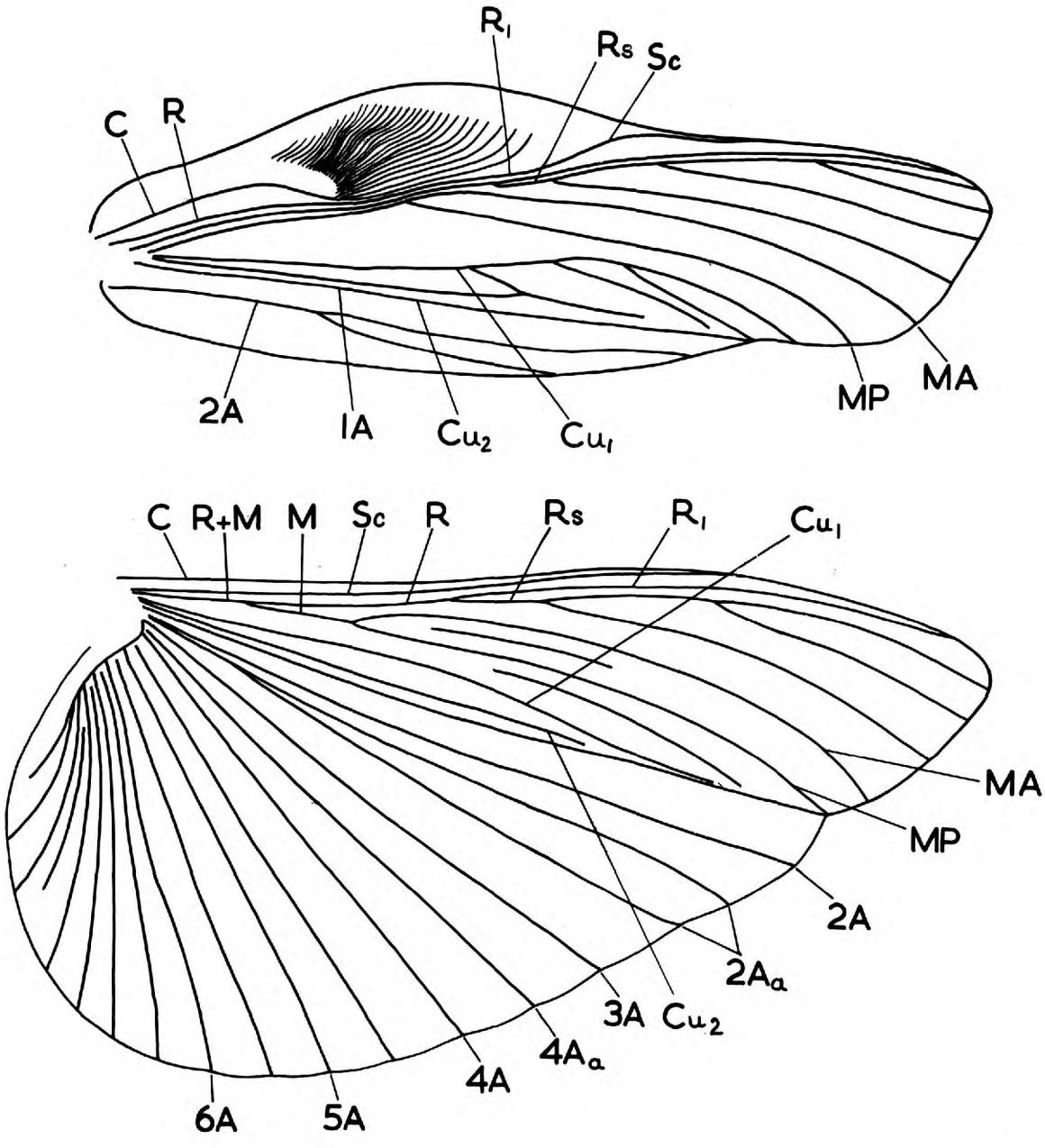


Fig.25f. The wings of Lamarckiana.

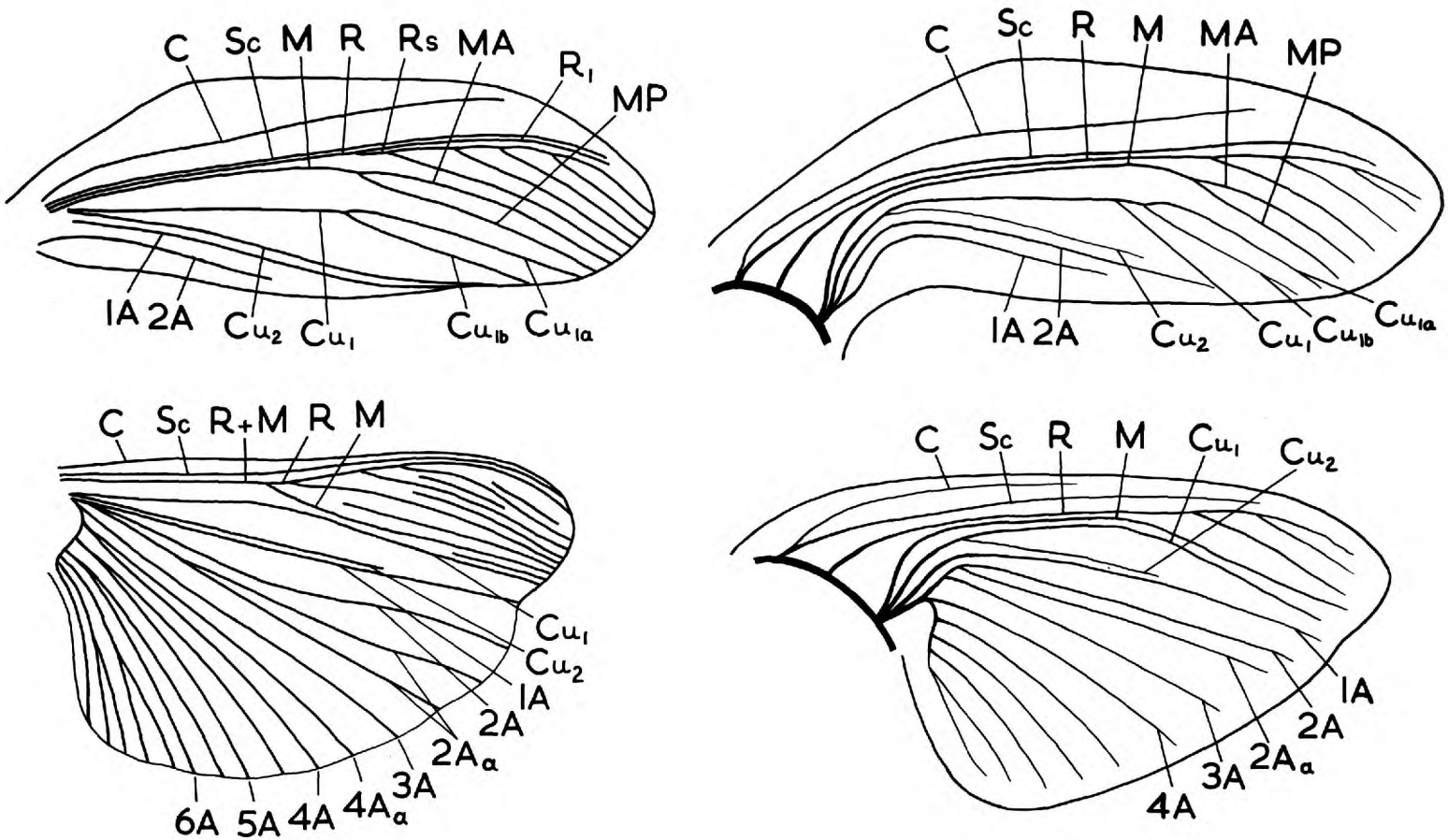


Fig.25h. The wings (left) and wing-pads of Teratodes.

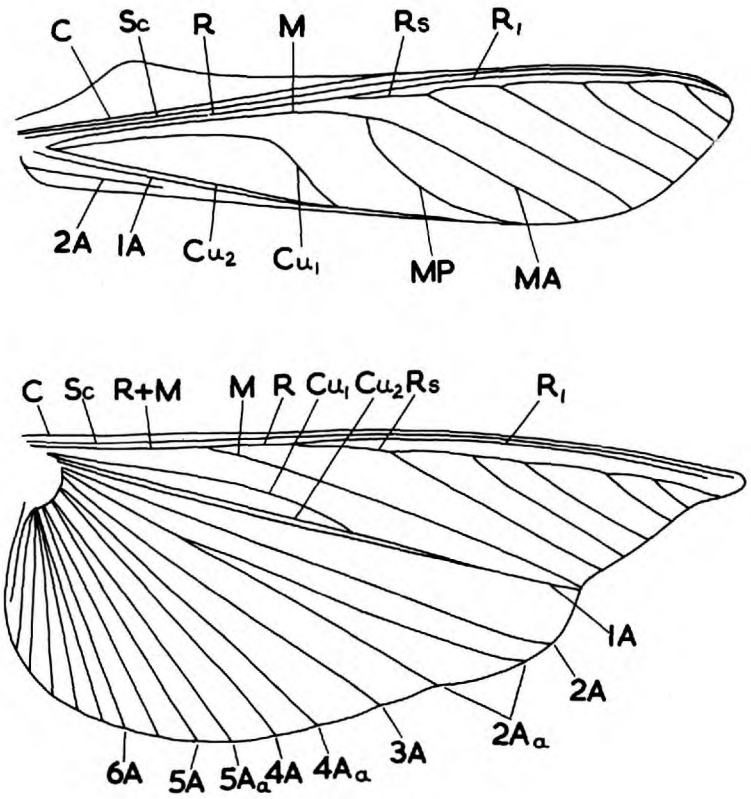


Fig.25j. The wings of Chorotypus.

X. ACRIDOIDEA - TETRIGIDAE

1. INTRODUCTION

The earliest work on the homologies of the veins of Tetrigid wings is that of Hancock (1902). This author describes and illustrates the wing-venation of Paratettix cucullatus Morse, Tettigidea parvipennis Morse, and Tettix gibbosus Hancock, basing his views largely on tracheae seen in the adult wings. Forbes (1937) gives a labelled drawing of the wings of a Tettigidea species, and Carpentier (1936) has repeated these observations on Acrydium subulatum Linnaeus.

The views of these authors, and those of Handlirsch (Schroeder, 1925) are tabulated in Fig. 26.

No fresh nymphs were available, but the wing-tracheation could be seen in preserved nymphs and in some adult wings.

2. THE SHAPE AND AREAS OF THE WINGS

(a) Fore wing.

The fore wings, when present, are always reduced to small, rather heavily sclerotized, structures, which are partly concealed by the backward prolongation of the pronotum. Their normal shape is lobiform, but occasionally they are elongate and relatively narrow (e.g. Otumba Morse).

(b) Hind wing.

The hind wings are usually well-developed and often extend beyond the apex of the abdomen; when flexed they are

NOMENCLATURE IN THIS WORK	SYMBOL	HANCOCK (1902)	HANDLIRSCH (1925)	FORBES (1933) & CARPENTIER (1936)
Costa	C	Costa	Costa	Costa
Subcosta	Sc	Subcosta	Subcosta	Subcosta
Radius	R	Radius	R	Radius
Media	M	Media	Rs	
Cubitus-one	Cu_1	Cubitus	Media	Media
Cubitus-two	Cu_2	First Anal	Cubitus	M + Cu
First anal	1A			Second plical
Second anal	2A			Ax_1

Fig. 26. Comparative table showing the nomenclatures used by various authors for the veins of Tetrigid hind wings.

shielded dorsally by the pronotum. The extended hind wing has the normal Orthopterous shape, with a relatively enormous anal area. The pre-anal part of the wing is reduced to a narrow anterior band.

3. THE VEINS

The veins of Tetrigid wings may be classified in the same way as those of the Pneumoridae, and the various types are defined under ~~this~~ that family (see p. 66 et seq.).

The typical venation of Tetrigid wings is illustrated in Fig. 27.

(a) The longitudinal veins.

(i) Primary veins.

THE COSTA (C)

There is no costa in the fore wing.

In the hind wing the costa is well-developed and lies along the anterior margin.

THE SUBCOSTA (Sc)

In the fore wing there is often a weakly developed subcosta in the central region of the wing.

The subcosta runs parallel to the costa in the hind wing; it often fuses with this vein before reaching the apex of the wing.

THE RADIUS (R)

The radius runs just behind the subcosta in the fore wing. This is also true in the hind wing: the two veins are closely pressed together for a large part of their length,

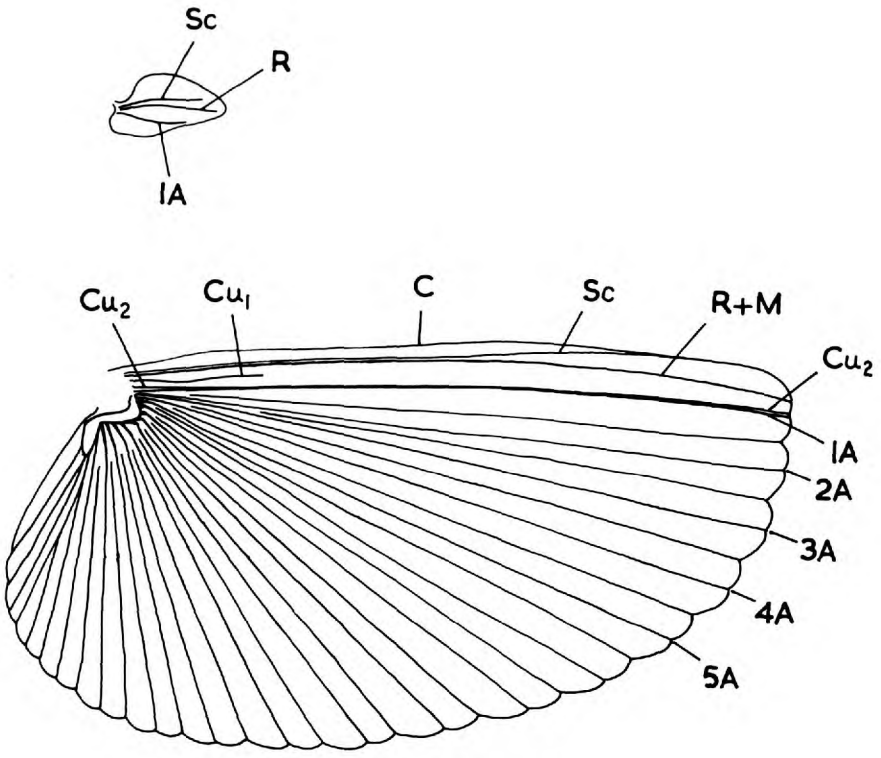


Fig.27. The wings of Eugavialidium.

becoming separated in the distal part of the wing. In the radial stem is also incorporated the media, which, however, often separates at the wing-apex.

THE MEDIA (M)

There is no media in the fore wing.

In the hind wing the media is completely fused to the radius for all or nearly all of its length.

THE CUBITUS (Cu)

This vein is absent from the fore wing.

In the hind wing the cubitus is divided from the base into two stems, Cu_1 and Cu_2. Cu_1 is a short vein, often less than a quarter of the wing-length; it frequently bends posteriorly and runs into Cu_2 at its extremity. Cu_2 is not very strongly developed but reaches the apex of the wing, running parallel to R M.

THE ANALS

In the fore wing there is a feebly developed first anal (1A) and additional anal veins are sometimes visible.

The first anal vein is strongly developed in the hind wing, where it is closely pressed against Cu_2 for almost the whole of its length. The two veins tend to separate slightly at the apex of the wing. The anal fan is supported by numerous radially-arranged veins in the usual manner. No definite homologies can be ascribed to them, and they are here called 2A, 3A, etc., consecutively, for descriptive purposes.

(ii) Secondary veins.

The only secondary veins in Tetrigid wings are the intercalary veins between the primary veins supporting the anal fan; they form the concave ribs of the fan, alternating with the convex anal veins. No other definite convexities or concavities are shown by Tetrigid wing-veins.

(b) The cross-veins.

Owing to the extreme reduction of the venation, there are no well-developed cross-veins in the fore wings, though there are frequently a number of very reduced ones in the posterior half.

All the areas of the hind wings are supported by numerous well-developed cross-veins, especially in the larger species.

(c) The archedictyon.

The anterior part of the fore wing is supported by an archedictyon of thick, heavily sclerotized veins, and there is a tendency for this to develop in parts of the posterior region of the wing. It is probable that this archedictyon is a secondary structure, arising from the extreme reduction of the fore wings.

There is no archedictyon in the hind wing.

XI. ACRIDOIDEA - CONCLUSIONS

On the whole the Acridoidea have an extremely uniform wing-venation. The only exception to this is found in the Tetrigidae where the wings are highly modified and bear little resemblance to the normal Acridoid form. The other four families will therefore be considered first, and the Tetrigidae will be treated later.

The wings of the Locustopsidae, Pneumoridae, Acrididae, and Eumastacidae, are characterized by the following features:-

1. The close approximation of the more proximal regions of Sc, R, and M (but not Cu) in the fore wing.

2. The basal fusion of R and M in the hind wing.

3. A tendency towards the reduction of Cu_2.

The Pneumoridae have a more primitive wing-venation than the other three families, as shown by the following features:-

1. The archedictyon is more extensive, especially in the hind wing.

2. Cu_1 and Cu_2 retain their primitive convexity and concavity in the fore wing.

3. The bifurcation of Cu is rather more distal.

It should also be mentioned that the anal lobe of the Pneumorid hind wing is developed only to half the extent of that of the other three families, and there is no anal hinge in

the fore wing.

Acridid wings are more specialized than those of the Eumastacidae in the following respects:-

1. Sc, R, and M, are more closely approximated in the fore wing than in most Eumastacidae.

2. Intercalary veins are generally better-developed.

3. Cu_2 is further reduced in the hind wing.

4. R_1 and the main stem of R_s are more closely approximated, especially in the fore wing.

The Eumastacidae, on the other hand, show some venational features which are specialized when compared with the Acrididae:-

1. M is unbranched in the hind wing.

2. Cu_1 is reduced in the hind wing.

3. There is a posterior ambient vein along the margin of the anal lobe of the hind wing: this is probably a specialization.

An important diagnostic feature of the Eumastacid fore wing is the unbranched Cu_1. This vein is almost always two- or three-branched in the Acrididae and Locustopsidae.

As there has been much doubt as to whether the fossil family Locustopsidae is allied to the Acrididae or not (see Handlirsch, 1939; Zeuner, 1942), a list is given below of venational features of the fore wing which are common to both.

1. The submarginal costa.

2. The pectinate radial sector.

3. The basal bifurcation of the cubitus.

4. The reduced Cu_2.

5. The intercalary veins in the distal half.

6. The archedictyon towards the base.

7. The three-branched Cu_1.

8. The nature of the convexities and concavities.

Of these features, Nos. 1 - 3 are Saltatorian, No. 4 is Acridoid, and the rest, in combination, suggest that the Locustopsidae are more closely related to the Acrididae than to any other Acridoid family.

The venation of the Locustopsid fore wing differs from that of the Acrididae in the following respects:-

1. The media is three-branched (This is the case in some members of the Acridid subfamily Ommexechinae, but here the branching is of a different nature.).

2. The submarginal part of the costa is shorter.

3. Sc, R, and M, are more separate from each other near the base.

4. The anal area is comparatively smaller.

5. R_1 and R_s are wider apart.

Also, the wing-length:body-length ratio is very much greater than that of most Acrididae.

The first of these features suggests that the Locustopsidae were not directly ancestral to the Acrididae.

The remaining family to be considered, the Tetrigidae, is typified by a uniform but very modified wing-venation which has practically nothing in common with the other Acridoid families. The only significant feature of Tetrigid venation which is found in the remaining families is the fusion of R and M in the hind wing; this is therefore a universal Acridoid feature, though not a diagnostic one. The ~~alial~~ alary features by which the Tetrigidae differ from the remaining Acridoidea are as follows:-

1. The invariable reduction of the fore wings to heavily-sclerotized, punctured flaps.

2. The reduction of the pre-anal part of the hind wing, none of the pre-anal veins being branched (ignoring the basal division of Cu into Cu_1 and Cu_2).

3. The reduction of Cu_1, which does not extend into the distal half of the hind wing.

4. The close approximation of Cu_2 and 1A in the hind wing.

5. The close approximation of Sc and R M in the proximal half of the hind wing.

XII. TRIDACTYLOIDEA - TRIDACTYLIDAE

1. INTRODUCTION

The highly specialized wing-venation of this family has received little attention in the past. Forbes (1932) considered them to be a further development in the line of the Tetrigidae. The only work on the homologies of the veins is that of Carpentier (1936), who gives a labelled drawing of the wings of Tridactylus thoracicus Guérin-Méneville and describes the venation of this and other species of Tridactylidae. No tracheation studies have so far been carried out on Tridactylid wings and as no nymphs were available for the present work the account given here is brief and merely descriptive; the veins are named to facilitate the description and the homologies suggested must be regarded as tentative until the tracheation of the wings has been investigated.

A comparison between the nomenclature used here and that of Carpentier is given in Fig. 28.

2. THE SHAPE AND AREAS OF THE WINGS.

Tridactylid fore wings are reduced to short, more or less elliptical lobes. They are fairly heavily sclerotized and are almost devoid of venation.

The hind wings are often well-developed. The area anterior to Cu_2 is well-sclerotized, especially in Rhipipteryx,

NOMENCLATURE IN THIS WORK	SYMBOL	CARPENTIER (1936)
Subcosta	Sc	Subcosta
Radius	R	Radius
Media	M	
First anal	1A	Axillary

(a) Fore wing.

NOMENCLATURE IN THIS WORK	SYMBOL	CARPENTIER (1936)
Subcosta	Sc	Subcosta
Media	M	Radius
Cubitus-one	Cu_1	Media
Cubitus-two	Cu_2	Cubitus
First anal	1A	Second plical

(b) Hind wing

Fig. 28. A comparison between the nomenclature used in this work for Tridactylid wing-veins, and that of Carpentier (1936).

the remainder of the wing being membranous. In shape, the extended hind wing is like a fan, and when at rest folds in the usual Orthopterous manner.

3. THE VEINS

The venation of each wing will be described separately.

(a) Fore wing.

The fore wing has lost most of its venation (see Fig. 29), but two veins can generally be distinguished. The first of these runs close to the anterior wing-margin at its base, then curves down towards the centre of the wing, and finally bends upwards towards the wing-margin again. It is very likely that this vein is the subcosta and it is regarded as such here. In the males of some species of Tridactylus Sc bears a number of ventral stridulatory teeth. Behind the subcosta is a vein running along the longitudinal axis of the wing, here regarded as the radius.

In Rhipipteryx these are the only two veins visible in the fore wing, but in Tridactylus there is often a third vein, arising a short distance behind R and diverging from it towards the posterior wing-margin. This vein is regarded here as the first anal.

(b) Hind wing.

There is a feebly developed costa supporting the basal part of the anterior margin of the hind wing. In Tridactylus a rudimentary subcosta is visible at the base of the wing, just

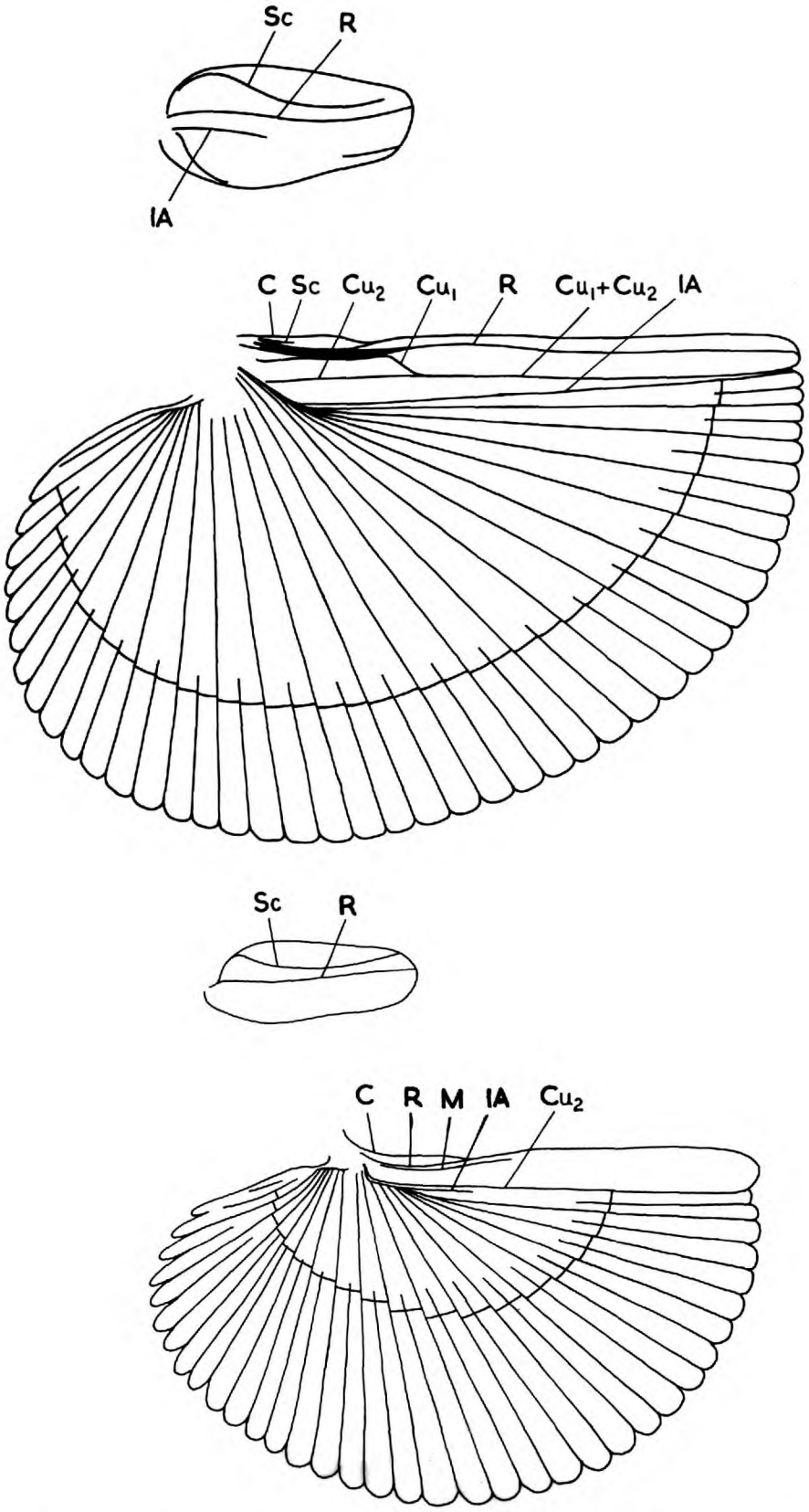


Fig.29. The wings of Tridactylus thoracicus (above) and Rhipipteryx chopardi Willemse.

behind the wing-margin. R, M, and Cu_1, are all fused or closely associated at the base of the wing, separating about a third of the way along it. The radius occupies a submarginal position in Tridactylus, but supports the distal part of the anterior wing-margin in Rhipipteryx. The media becomes obsolete in the more distal part of the wing. Cu_1 has disappeared in Rhipipteryx, but in Tridactylus it bends sharply down to fuse with Cu_2. The latter vein forms the posterior boundary of the unfolded, sclerotized, part of the hind wing. 1A lies a short distance behind Cu_2, gradually converging with it in Tridactylus, but rapidly becoming obsolete in Rhipipteryx. The remainder of the hind wing is supported by the radially-arranged anal veins of the anal fan.

There are no accessory veins in Tridactylid wings, but intercalary veins are found alternating with the anal veins in the anal fan. Ambient veins are not developed, and cross-veins (except for a single row in the anal fan) are only found in Tridactylus, where there are often a few between R and Cu_1+Cu_2, and between Cu_2 and 1A.

The above description applies only to species in which the hind wings are fully developed; brachyptery is common and is accompanied by reduced venation.

XIII. TETTIGONIOIDEA - PROPHALANGOPSIDAE

1. INTRODUCTION

The wing-venation of this family has been dealt with fairly fully by Zeuner (1939), but, as the homologies attributed to the veins by this author differ slightly from those in this work, a brief account of Prophalangopsid wing-venation is given here. The relationships of the Liassic Geinitziinae are uncertain and this group is not treated here.

The Prophalangopsidae, as delimited by Zeuner (op. cit.), is almost entirely a fossil family, there being only three living species, Prophalangopsis obscura, Cyphoderris monstrosa Uhler, and C. buckelli Hebard. Of these three species, P. obscura is fully-winged and the Cyphoderris species are brachypterous in the male and microalate in the female. Only one specimen of Prophalangopsis is known; this is a male, about a hundred years old, and in bad condition. It was found in India and presented to the British Museum in 1861.

A comparison between the nomenclature used in this work and that of Zeuner (op. cit.) is given in Fig. 30.

2. THE TRACHEATION OF THE NYMPHAL WING-PADS

No fresh nymphs of Cyphoderris were available, but the tracheation could be seen in the adult wings.

NOMENCLATURE IN THIS WORK	SYMBOL	ZEUNER (1939)	SAUSSURE (1898)
Costa	C	Costa or Costa secans	
Subcosta	Sc	Subcosta	Humeral
Radius	R	Radius	
Radius-one	R_1		Discoidal
Radial sector	R_s		Median
Media	M	Media	Ulnar
Cubitus-one	Cu_1	Cubitus	
Cubitus-two	Cu_2	First anal	
First anal	1A	Second anal	
Second anal	2A	Third anal	

Fig. 30. A comparison between the nomenclature used in this work for the veins of the fore wings of Prophalangopsis and those of Zeuner (1939) and Saussure (1898). (In the hind wing Zeuner's views are identical with those expressed in the present work; Saussure gave no nomenclature for Prophalangopsid hind wings.)

3. THE SHAPE AND AREAS OF THE WINGS

(a) Fore wing.

The fore wings vary in shape from being relatively long and narrow, as in Hagla gracilis (about four times longer than broad - see Fig. 31), to being lobe-like, as in Prophalangopsis obscura (see Fig. 32), or almost circular, as in Cyphoderris (see Fig. 33).

The areas of the fore wings are easily named using the Comstock-Needham System (see Fig. 34).

(b) Hind wing.

The only complete fully-developed hind wing known is that of Prophalangopsis, but what fragments remain of fossil wings suggest that the shape found in this genus is typical of the family. As in the fore wing the areas are easily named and are shown in Fig. 34.

4. THE VEINS

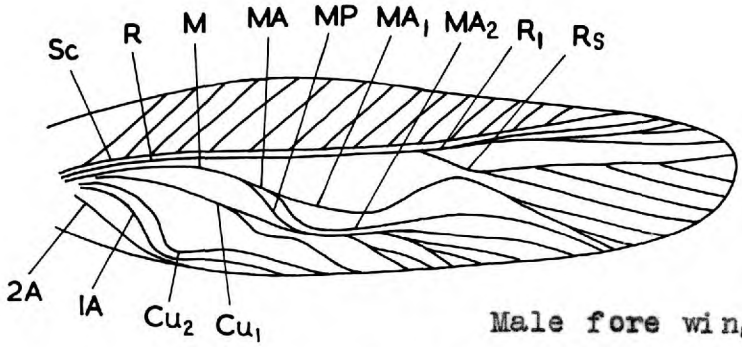
The veins of Prophalangopsid wings may be classified in the same way as those of the Pneumoridae, and the various types are defined under ~~this~~ that family (see p. 66 et seq.).

(a) The longitudinal veins.

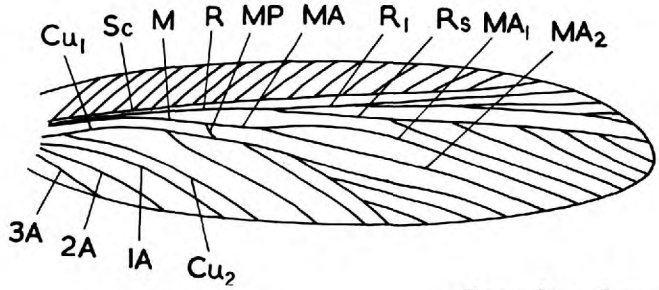
(i) Primary veins.

THE COSTA (C)

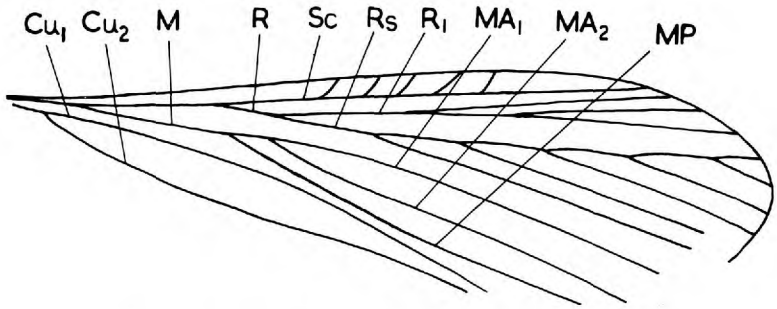
In the fore wings of Cyphoderris no well-developed costa is present, but the most proximal of the anterior branches arising from the subcosta have a tracheal supply from a short



Male fore wing.



Female fore wing.



Part of the hind wing.

Fig.31. The wings of Hagla gracilis.

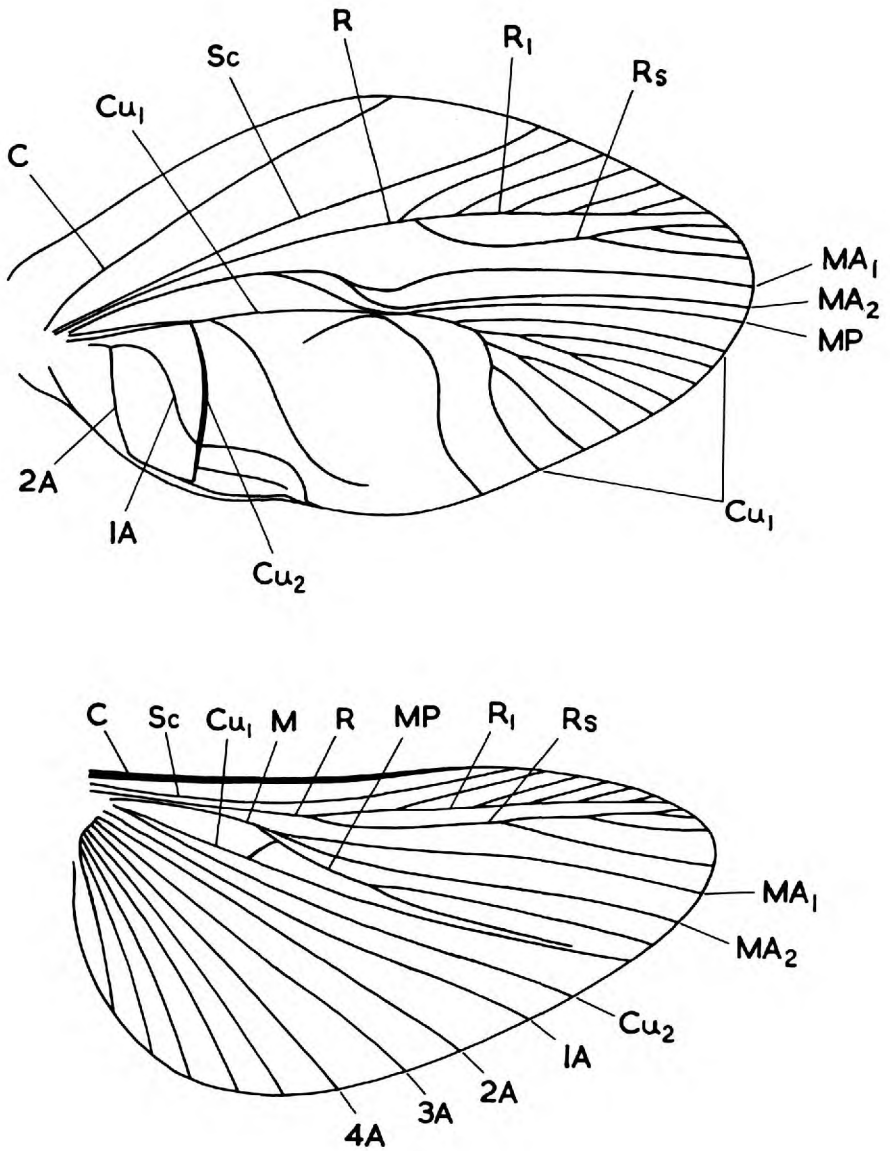


Fig.32. The wings of Prophalangopsis obscura.

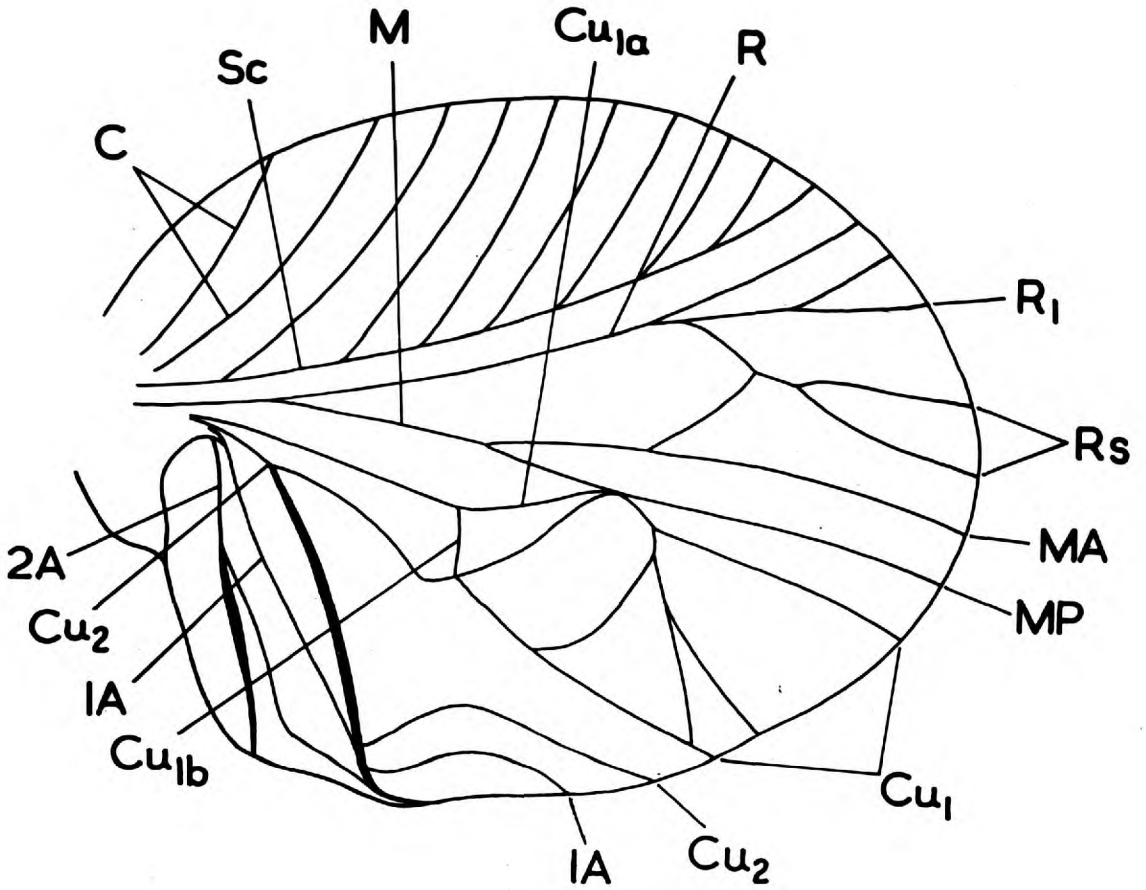
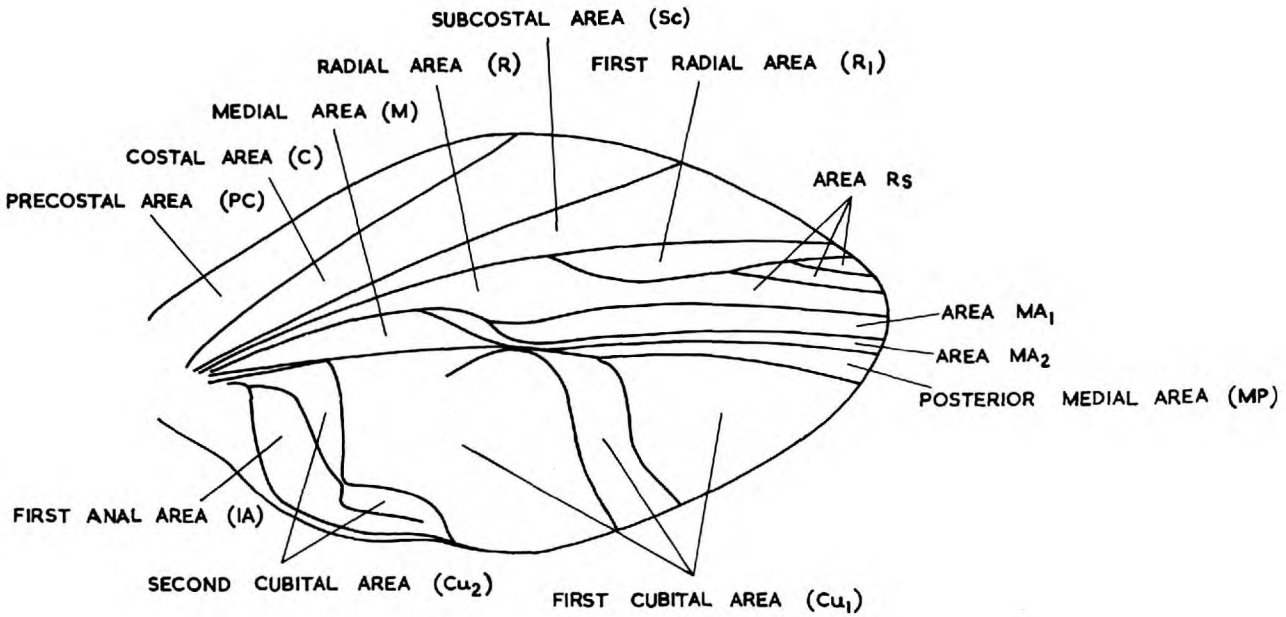


Fig.33. The fore wing of Cyphoderris, male.



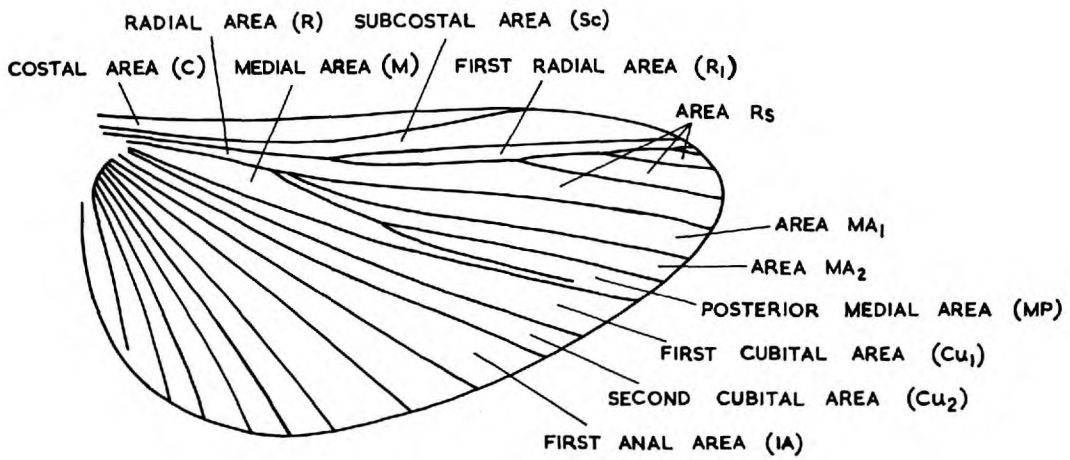


Fig.34a. The areas of the wings of Prophalangopsis.

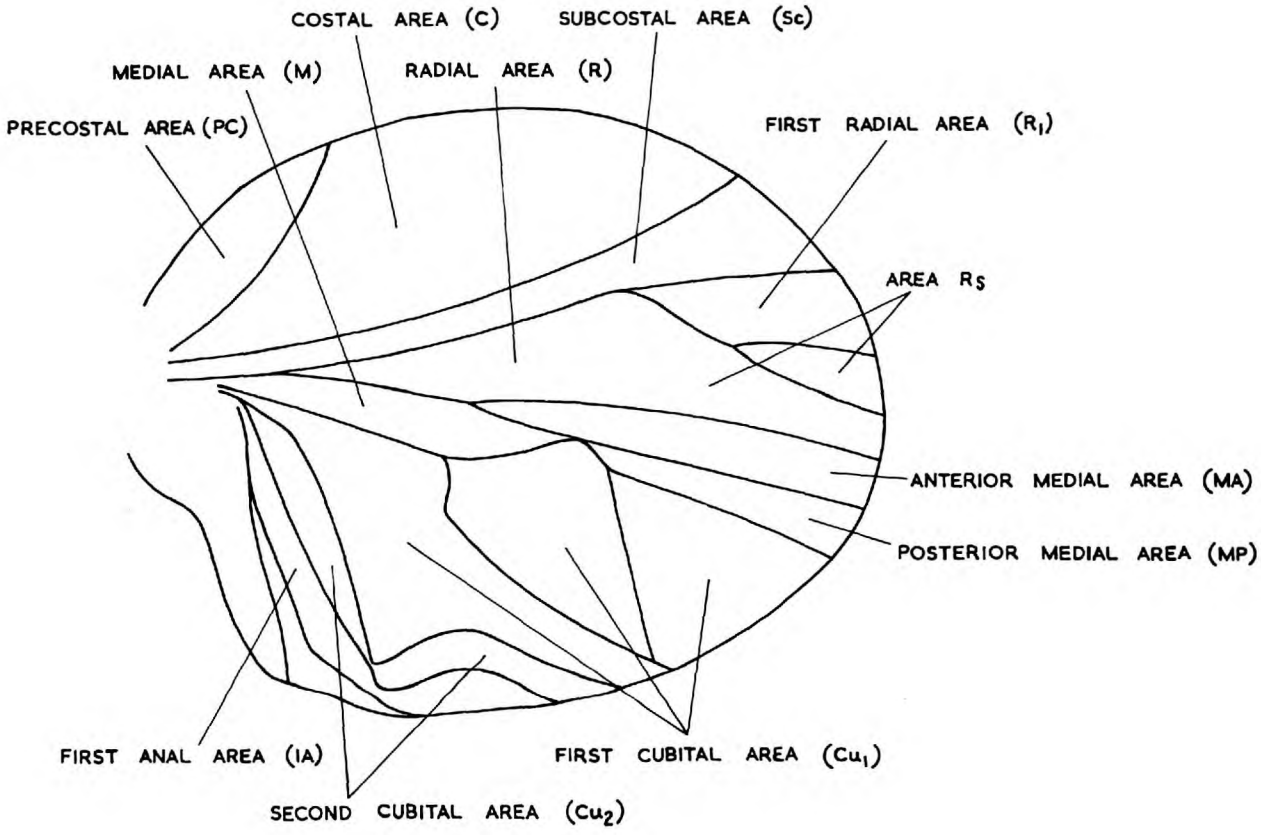


Fig.34b. The areas of the fore wing of Cyphoderris.

common trunk separate from the subcostal trachea, suggesting that these branches represent the costa. In the Prophalangopsis fore wing there is a strongly developed longitudinal vein in the area anterior to the subcosta; it is possible that this is the costa, but in the absence of tracheation studies it is impossible to be quite certain that it is not an accessory vein, especially as it is apparently crossed by the subcostal accessory branches.

In the fossil forms it is probable that the costa is represented by the most proximal subcostal branches, as in Cyphoderris.

In all known Prophalangopsid hind wings there is a normally developed costa along the anterior margin, convex in Prophalangopsis.

THE SUBCOSTA (Sc)

In the fore wing this vein always lies some distance behind the anterior margin; the area thus delimited is supported by its numerous anterior accessory branches.

In the hind wing the subcosta runs just behind the costa.

The subcosta is normally concave in both pairs of wings.

THE RADIUS (R)

This vein runs just behind and parallel to the subcosta. It becomes divided, generally about midway along the wing, into two branches, R_1 and R_s; the former bears a number

of anterior branches, and the latter a number of posterior ones. In the fossil forms the R_s branches are more numerous than the branches of R_1; in Prophalangopsis, however, the reverse is the case.

The radius is convex in both pairs of wings.

THE MEDIA (M)

The media lies just posterior to the radius. It divides into two branches, MA and MP, and the anterior one typically divides again (forming MA_1 and MA_2). This branching usually occurs in the proximal part of the wing, but in Cyphoderris the media divides at a central point; in this genus, which has a reduced venation, MA is unbranched. In the fore wing MP normally becomes fused for part of its length to Cu_1 or Cu_{1a}; in the hind wing this is probably also true of Pamphagopsis maculata (see Fig. 36), and possibly so in Prophalangopsis (see below), but MP and Cu_1 appear to be quite free in Hagla gracilis.

The media and its branches show no definite and constant convexities or concavities.

THE CUBITUS (Cu)

This vein divides at its base into two branches, Cu_1 and Cu_2. In the fore wing Cu_1 gives rise to a variable number of further branches. In the hind wing it appears to be unbranched in Hagla gracilis, but in Pamphagopsis maculata (according to Martynov's figure, reproduced in Fig. 36) Cu_1 gives rise to an anterior branch (Cu_{1a}) which fuses for part

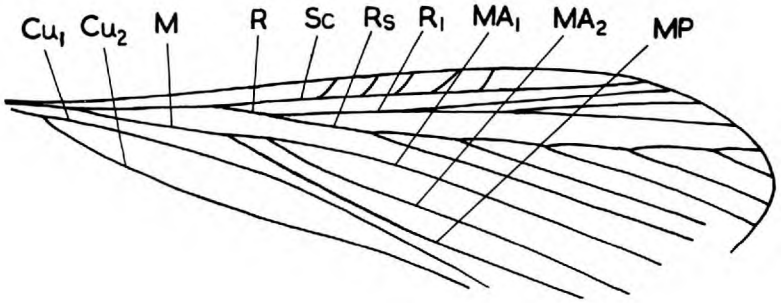


Fig.35. Part of the hind wing of Hagla gracilis.

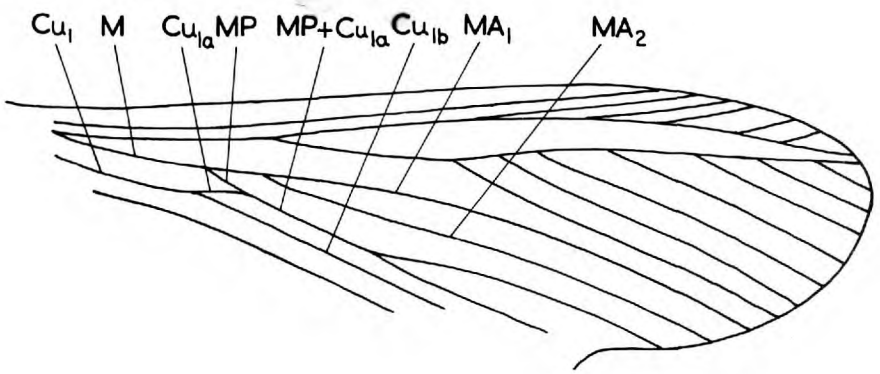


Fig.36. Part of the hind wing of Pamphagopsis maculata. Partly after Martynov (1925).

of its length with MP. This may also be the case in the hind wings of Prophalangopsis, where one of the apparent cross-veins between Cu_1 and the base of MP is rather more strongly developed and oblique than the others, and may therefore be Cu_{1a} (this vein is shown in Fig. 32).

Cu_2 is unbranched in both pairs of wings. In the male fore wing it forms the stridulatory rib and bears a row of teeth on the underside.

Cu_1 and Cu_2 tend to be convex and concave respectively in the fossil fore wings; in the fore wings of the modern forms these veins show no definite convexities or concavities. Cu_1 is concave in the hind wings of Prophalangopsis.

THE ANALS

There are generally two or three anal veins in Prophalangopsid fore wings. The first anal (1A) sometimes forms the most posterior part of the stridulatory rib (e.g. Prophalangopsis, Cyphoderris, Aboilus columnatus Martynov).

In the hind wings of Prophalangopsis the anal veins are of the normal Orthopterous type: they are radially-arranged and support the anal fan.

The first anal is convex in the fore wings of Cyrtophyllites, Prophalangopsis, and Cyphoderris, and in the hind wings of Prophalangopsis.

(ii) Secondary veins.

A. Intercalary veins.

These veins are not very common in Prophalangopsid

wings. There is, however, a tendency for their development between the branches of R_s, M, and Cu, in Zalmona brodiei (fore wing) and, according to Martynov's figure (Martynov, 1934, Fig. 1963), there are intercalary veins between the branches of R_s and M in Aboilus columnatus (fore wing). There are a few rather feebly developed intercalary veins in both fore and hind wings of Prophalangopsis, again between the branches of R_s, M, and Cu.

B. Accessory veins.

There ~~are~~ is always a number of accessory veins in Prophalangopsid wings. In the fore wing the subcosta invariably gives rise to a row of anterior accessory branches. This also applies to R_1 in both pairs of wings, and in some fore wings there are also some anterior accessory branches arising from the main stem of the radius.

In the fore wing Cu_1 bears a number of accessory branches, and in Cyphoderris this vein divides into a definitive Cu_{1a} and Cu_{1b}, as in the Tettigoniidae.

The anal veins are normally undivided, but in Cyphoderris 2A sometimes bears an accessory branch.

(b) The cross-veins.

The arrangement of the cross-veins is very characteristic of most of the fossil Prophalangopsidae. In many of the areas of the fore wing they are very numerous and close together, giving the venation a web-like appearance. This is particularly

true of the radial, medial, and cubital, areas.

In the more advanced fossil form Zalmona bradiei this feature is not so prominent, and it has practically disappeared in the modern species.

In the known hind wings the cross-veins are developed normally.

(c) The archedictyon.

There is no primitive archedictyon in Prophalangopsid wings, though there is a tendency towards its secondary development in the reduced fore wings of Cyphoderris.

It is possible that in the Prophalangopsidae the intercalary veins were formed from the cross-veins and not from the archedictyon.

XIV. TETTIGONIOIDEA - GRYLLACRIDIDAE

1. INTRODUCTION

The wing-venation of this family has been studied by Karny (1925, 1930), and has been discussed more recently by Zeuner (1939); the present account will therefore be brief, Karny's nomenclature differing in no important respect from that used in this work.

A comparison between the opinions of various authors is given in Fig. 37.

2. THE TRACHEATION OF THE NYMPHAL WING-PADS

The tracheation of the nymphal wing-pads of Gryllacris has been fully dealt with by Karny (1925). His figures (see Fig. 38) show that the veins in the precostal area of the fore wing can be regarded as accessory branches of the costa, as their tracheae arise from the costal trachea. The tracheation also shows clearly the fusions which have taken place between R, M, and Cu.

3. THE SHAPE AND AREAS OF THE WINGS

Gryllacridid fore wings (see Fig. 39) normally take the form of more or less elongate lobes, often only about twice as long as broad. The hind wings are generally ~~cycloid~~ semi-circular.

The areas of Gryllacridid wings are easily named using the Comstock-Needham System; an example is shown in Fig. 40.

NOMENCLATURE IN THIS WORK	SYMBOL	HANDLIRSCH (1925)	KARNY (1930)	ZEUNER (1939)	CHOPARD (1949)
Costa	C		Costa	Costa secans	Costa
Subcosta	Sc	Subcosta	Subcosta	Subcosta	Subcosta
Radius-one	R_1	R	R	R	R
Radial sector	R_S	R_S	R_S	R_S	R_S
Media	M	Media	Media	Media	Media
Cubitus-one	Cu_1	Cubitus	Cu	CuA	Cu Cup
Cubitus-two	Cu_2		CuS	CuP	
First anal, etc.	1A, etc.	Anals	Anals	Anals	Anal, etc.

(a) Fore wing

NOMENCLATURE IN THIS WORK	SYMBOL	HANDLIRSCH (1925)	KARNY (1930)	FORBES (1933)	CHOPARD (1949)
Costa	C		Costa		
Subcosta	Sc		Subcosta	Subcosta	Subcosta
Radius-one	R_1	R	R	Radius-one	R
Radial sector	R_S	R_S	R_S	Radial sector	Media
Media	M		Media		
Cubitus-one	Cu_1	Media	Cu	M_{1+2}	Cubitus
Cubitus-two	Cu_2	Cubitus	CuS	$Cu+M_{3+4}$	Anal
First anal, etc.	1A, etc.	Anals	Anals	First plical, etc.	Axillaries

(b) Hind wing

Fig. 37. Comparative table showing the nomenclatures used by various authors for Gryllacridid wing-veins.

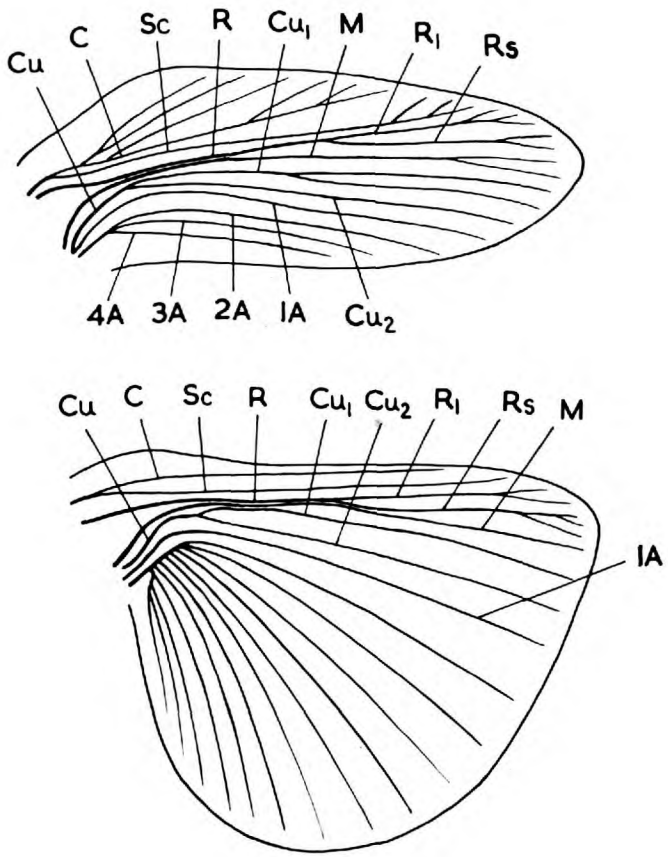


Fig.38. The tracheation of the nymphal wing-pads of Gryllacris signifera (Stoll). After Karny (1925).

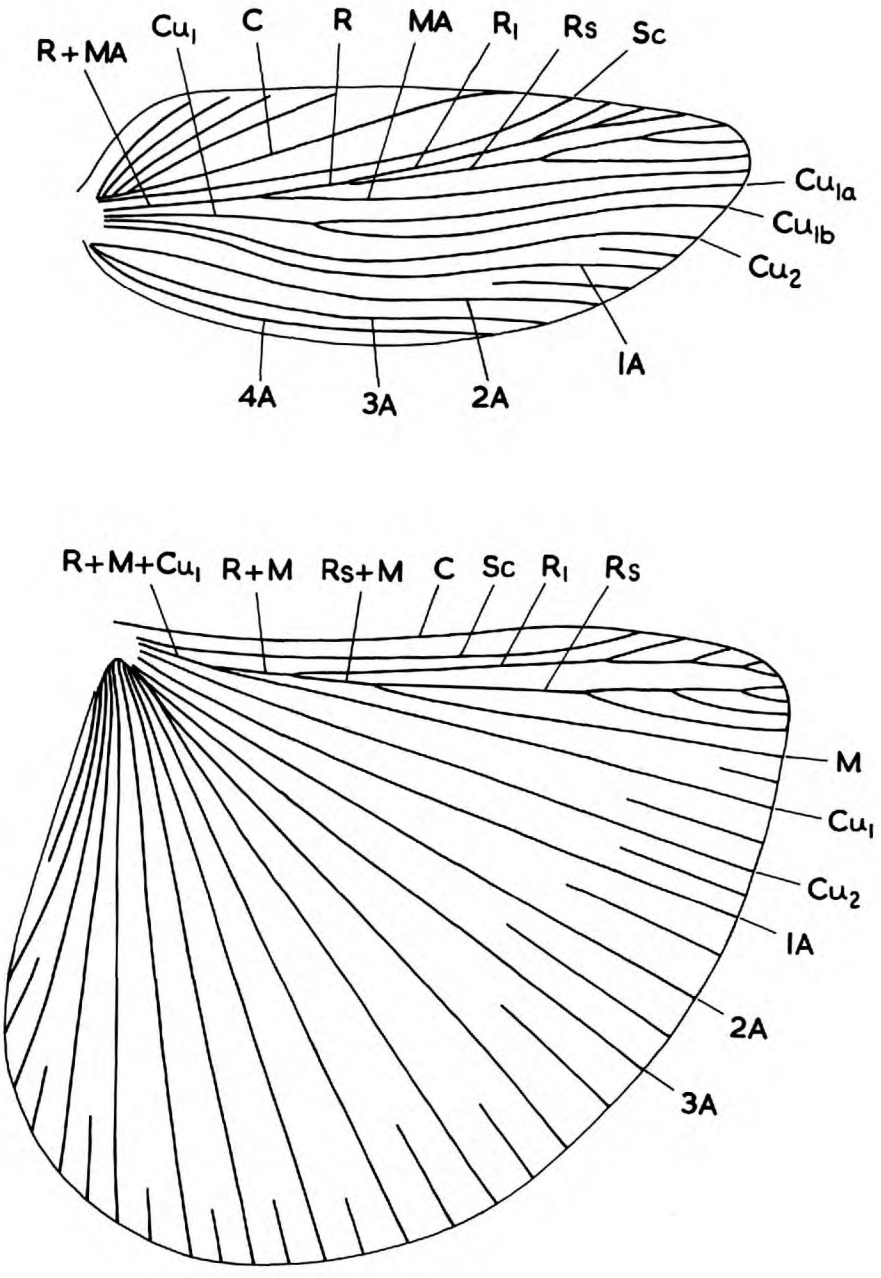


Fig.39. The wings of Gryllacris.

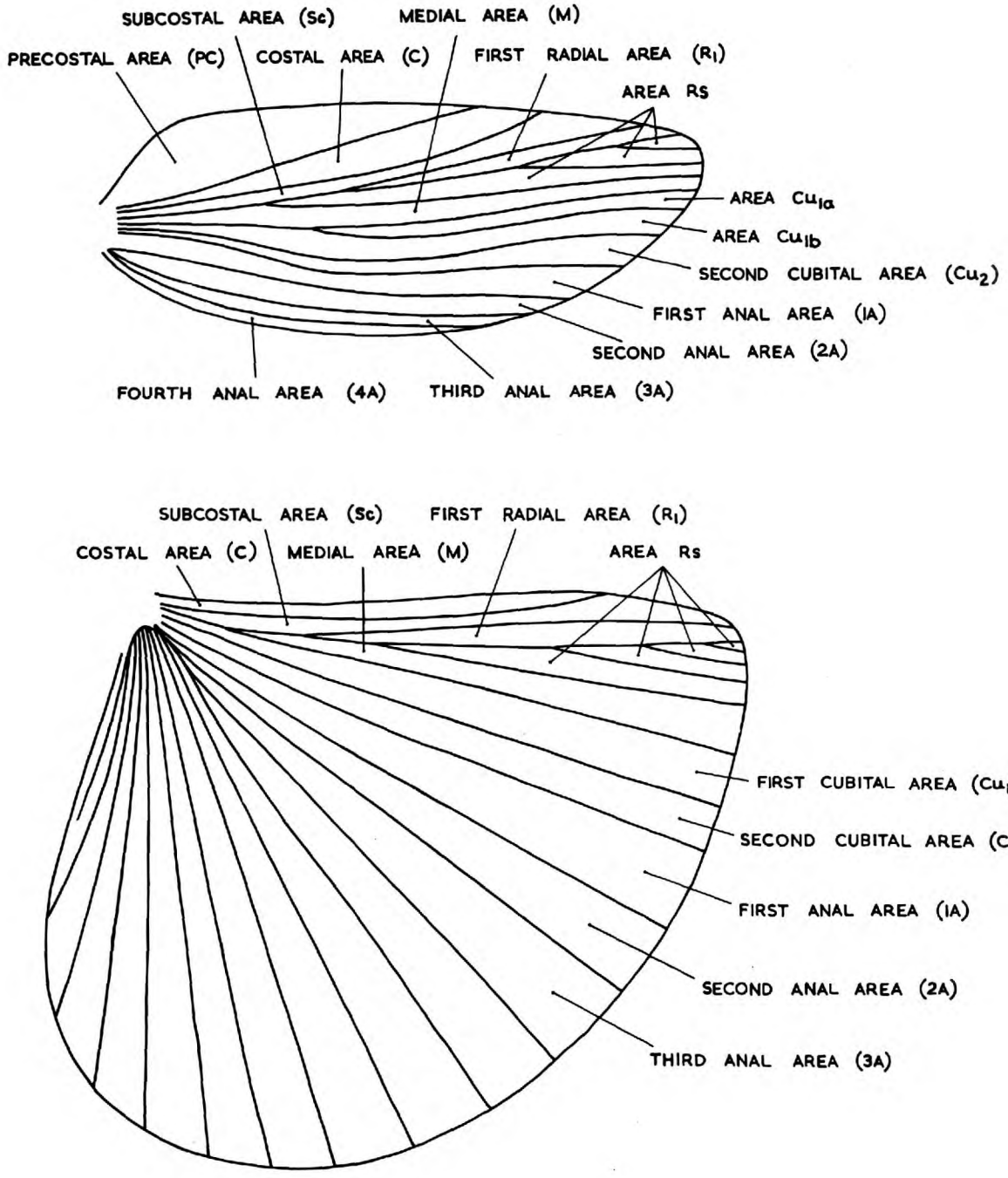


Fig.40. The areas of Gryllacridid wings.

4. THE VEINS

The veins of Gryllacridid wings may be classified in the same way as those of the Pneumoridae, and the various types are defined under ~~this~~ that family (see p. 66 et seq.).

(a) The ambient veins.

There are no well defined ambient veins in Gryllacridid wings. There is often, however, a continuation of the costa round the apex of the hind wing, and this may be looked upon as a short ambient vein. A feebly developed vein of a similar nature is sometimes found in the fore wing.

(b) The longitudinal veins.

(i) Primary veins.

THE COSTA (C)

There is a well-developed submarginal costa in the fore wing; it reaches the anterior margin about halfway along its length, or sometimes a little nearer the apex. The costa frequently bears a number of anterior accessory branches arising from near its base.

In the hind wing the costa (when present) lies along the anterior margin. It tends to be convex in both pairs of wings.

THE SUBCOSTA (Sc)

This vein runs a short distance behind and parallel to the costa in both pairs of wings. It is often concave in the fore wing but usually shows no tendencies in this respect in the hind wing.

THE RADIUS (R)

In both pairs of wings this vein lies close behind the subcosta. It becomes divided into two branches, R_1 and R_s; the former generally bears anterior accessory branches , and the latter is normally branched in the usual posterior pectinate manner.

The radius is often convex in the fore wing and sometimes tends to be so in the hind wing.

THE MEDIA (M)

This vein is fused to the radius for part of its length in the more specialized fore wings, usually at the base but sometimes with a short length of R_s. It is either unbranched or bifurcate (rarely three-branched), and the posterior branch (when present) often fuses with Cu_1. On the basis of this frequent fusion, and the fact that M is only bifurcate in the less specialized fore wings, it is probable that, when the media is a single stem, it only represents MA, MP being completely lost or fused to Cu_1. This is regarded as being the case here (see p. 48).

In the hind wing the fusion of the media and radius is often even more advanced than in the fore wing: in the most specialized forms the media is completely fused to both the main stem of the radius and part of the stem of R_s, thus appearing to be the most basal of the R_s branches. It is normally unbranched in the hind wing.

The media shows no definite convexity or concavity.

THE CUBITUS (Cu)

In both pairs of wings this vein divides at the base into Cu_1 and Cu_2. Cu_2 is never branched, but Cu_1 is frequently bifurcate in the fore wing. In the hind wing a certain amount of basal fusion between Cu_1 and R+M is common.

The cubitus shows no definite convexity or concavity.

THE ANALS

There are three or four parallel anal veins behind the cubitus in the fore wing; in the hind wing the anal veins are numerous, supporting the extensive anal fan.

The anal veins tend to be slightly convex in the fore wing.

(ii) Secondary veins.

A. Intercalary veins.

There are often a few short intercalary veins in the fore wing, especially in the region of the media and cubitus. In the hind wing there are intercalary veins between most of the ribs supporting the cubito-anal fan.

B. Accessory veins.

The most characteristic accessory veins in Gryllacridid wings are the anterior basal branches of the costa in the fore wing. R_1 generally bears a few anterior accessory branches at its distal end in both pairs of wings. Accessory veins elsewhere are rare.

(c) The cross-veins.

Well-developed cross-veins are found throughout both pairs of wings, supporting all the areas between the veins.

(d) The archedictyon.

There is no true archedictyon in Gryllacridid wings.

XV. TETTIGONIOIDEA - ELCANIDAE

The wing-venation of this fossil family is adequately described in Section VI (p. 50 et seq.).

XVI. TETTIGONIOIDEA - TETTIGONIIDAE

1. INTRODUCTION

Very little work has been published in the past on Tettigoniid wing-venation. Comstock and Needham (1899, and Comstock, 1918) gave illustrations of the nymphal tracheation of Conocephalus Thunberg and Scudderia Stal, but drew no conclusions regarding the adult venation. Vignon (1929) made some observations on Tettigoniid tracheation, giving diagrams of the nymphal wing-pads of Tettigonia, Stilpnochlora Stal, and Ephippitytha Audinet-Serville. In 1938 Mu-Lien Hsueh published an illustrated paper on the tracheation and venation of Gampsocleis gratiosa, a brachypterous species. A number of observations are made by Zeuner (1939) on Tettigoniid venation, especially that of the fore wing, in which he distinguishes four basic venational types. This is the most comprehensive and probably the most recent work on the subject.

The correspondence between the nomenclatures of various authors is shown in Fig. 41.

2. THE TRACHEATION OF THE NYMPHAL WING-PADS

(a) Fore wing-pad.

The wing-pad tracheation of Tettigonia viridissima Linnaeus (see Fig 42) may be regarded as typical of the family. A costal trachea is developed, extending less than halfway along

NOMENCLATURE IN THIS WORK	SYMBOL	COMSTOCK (1918)	HANDLIRSCH (1925)	VIGNON (1929)	HSUEH (1938)	ZEUNER (1939)	CHOPARD (1949)	BRUNNER (1878)
Costa	C		Costa	Pseudocosta	Costa	Costa		Mediastinal
Subcosta	Sc	Subcosta	Subcosta	Subcosta	Subcosta	Subcosta	Subcosta	Anterior radial
Radius	R	Radius	Ra	Radius	Radius			Posterior radial
Radius-one	R_1	Radius-one	R	Radius-one		R	R	
Radial sector	R_s	Radial sector	R_s	Radial sector		R_s	R_s	
Media	M	Media	Media	Media	Media	Media		
Anterior media	MA			MA_2	M_{1+2}	MA	Media	Anterior ulnar
Posterior media	MP			1	M_{3+4}	MP	Cubitus	Posterior ulnar
Cubitus	Cu	Cubitus	Cubitus	Cubitus	Cubitus			
Cubitus-one	Cu_1	Cubitus-one		CuA	Cubitus-one			
Branches of Cubitus-one	Cu_{1a}			CuA_1		CuA		
	Cu_{1b}				Cu_{1a}	Cu_n		Vena dividens
Cubitus-two	Cu_2	Cubitus-two		CuP	Cubitus-two	First anal	Anal	
First anal	1A	A		First anal	First anal	Second anal	Axillaries	Vena plicata
Second anal	2A			Second anal	Second anal			

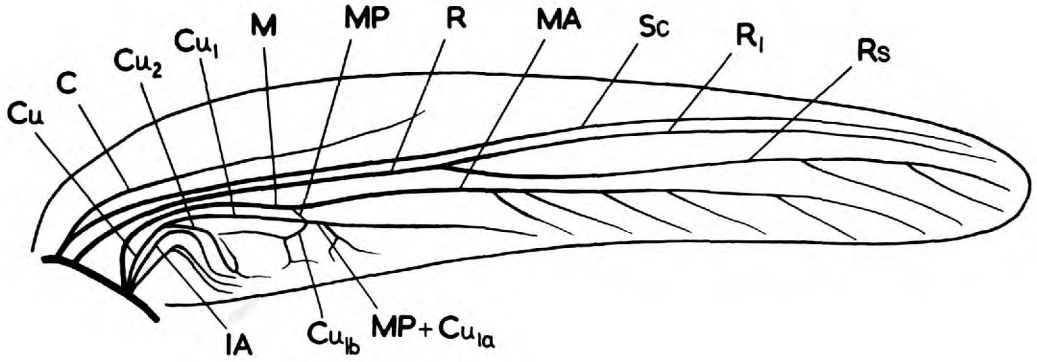
(a) Fore wing

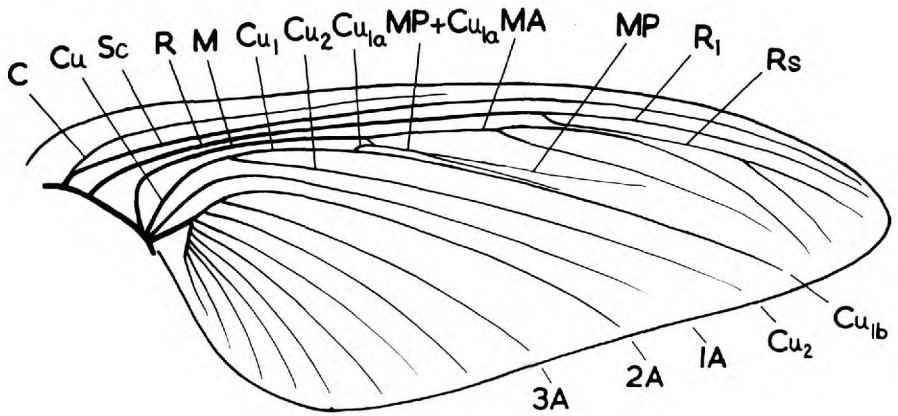
Fig. 41. Comparative table showing the nomenclatures used by various authors for Tettigoniid wing-veins.

NOMENCLATURE IN THIS WORK	SYMBOL	COMSTOCK (1918)	HANDLIRSCH (1925)	VIGNON (1929)	ZEUNER (1939)	CHOPARD (1949)	BRUNNER (1878)
Costa	C		Costa	Pseudocosta			Mediastinal
Subcosta	Sc	Subcosta	Subcosta	Subcosta	Subcosta	Subcosta	Anterior radial
Radius	R	Radius		Radius			Posterior radial
Radius-one	R_1	Radius-one	R	Radius-one	R	Radius	
Radial sector	R_s	Radial sector	R_s	Radial sector	R_s	Media	
Media	M	Media		Media	Media		
Anterior media	MA		Media	MA_2	MA		Anterior ulnar
Posterior media	MP			J	MP		Posterior ulnar
Cubitus	Cu	Cubitus	Cubitus	Cubitus	Cubitus		
Cubitus-one	Cu_1	Cubitus-one		CuA_1		Cu	Vena dividens
Branch of cubitus-one	Cu_{1a}			CuA_2			
Cubitus-two	Cu_2	Cubitus-two		CuP		Cup	Venae axillares
First anal	1A	First anal		First anal	First anal	Anal	
Second anal	2A				Second anal	Axillary	

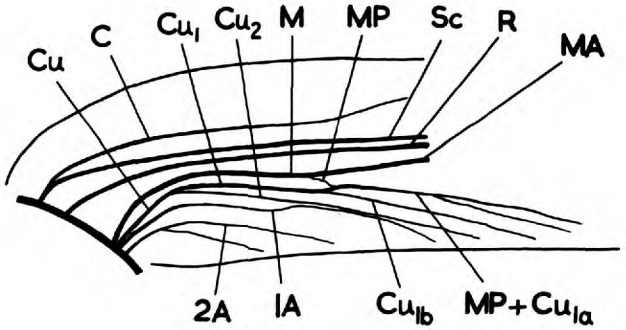
(b) Hind wing

Fig. 41. Comparative table showing the nomenclatures used by various authors for Tettigoniid wing-veins (contd.)





Male.



Part of the female fore wing-pad.

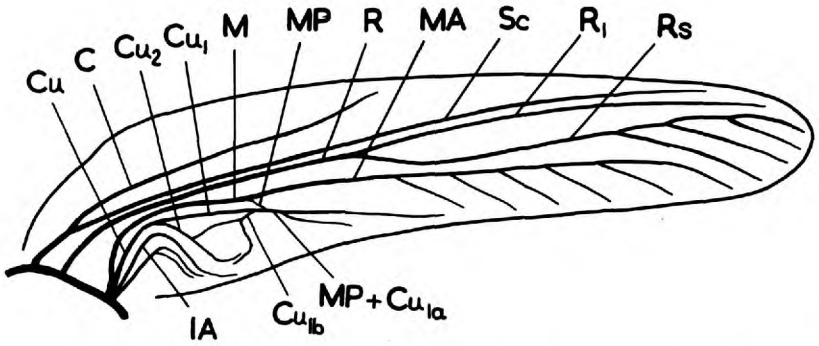
Fig.42. The tracheation of the nymphal wing-pads of Tettigonia viridissima.

the wing (as does the adult vein). The subcostal trachea is normal, reaching the tip of the wing-pad. These two tracheae are fused at their bases, forming a short common trunk which arises from the transverse basal trachea; they frequently bear anterior accessory branches.

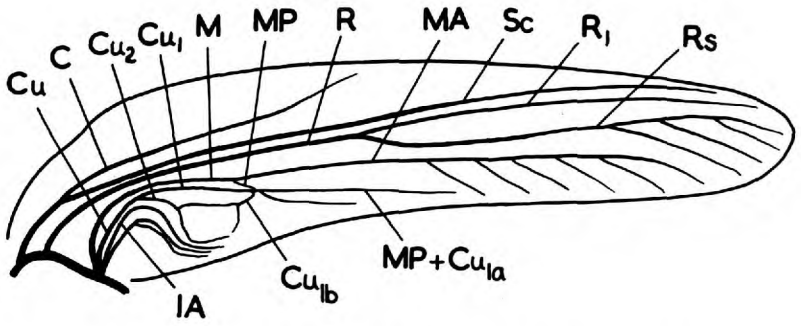
The radial trachea is typically divided into R_1 and a pectinate R_s. The point at which this division takes place varies, of course, in just the same way as in the adult wings.

In the remaining part of the fore wing-pad the tracheation is rather specialized. The medial trachea gives rise to a very small posterior branch near its base, representing MP; this fuses directly with Cu_{1a} or Cu_1. The remainder of the medial trachea, representing MA, is normally well-developed, extending nearly to the wing-tip. It usually bears posterior accessory branches. No trachea representing MP is shown in Comstock's diagram of Conocephalus (Comstock, 1918, Fig. 122) or Zeuner's illustrations of Decticus albifrons Linnaeus (Zeuner, 1939, Pl. XI, Figs. 3 and 4) and Mecopoda elongata Linnaeus (op. cit., Pl. X, Fig. 2); it is possible, therefore, that this trachea is sometimes absent. It is always present in Tettigonia viridissima and Decticus verrucivorus (Linnaeus) (Fig. 42a).

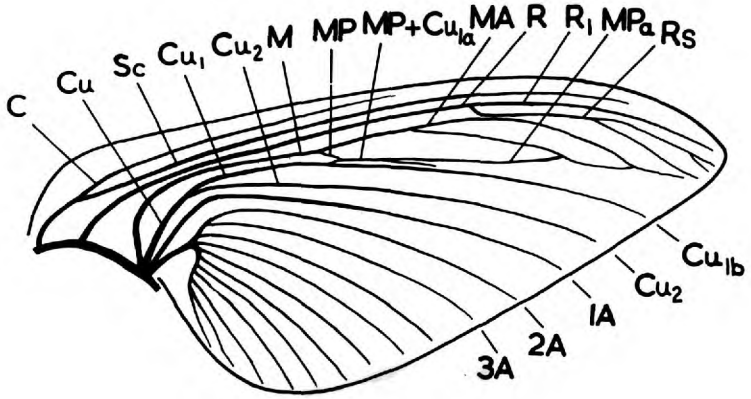
The cubital trachea is divided near its base into Cu_1 and Cu_2. Trachea Cu_1 again divides forming Cu_{1a} and Cu_{1b}, and the former of these branches is joined by MP to form $MP+Cu_{1a}$. Cu_{1b} runs straight to the wing-margin in the female, but in the male it bends back towards the base of the wing-pad and



Left male fore wing-pad.



Right male fore wing-pad.



Hind wing-pad.

Fig.42a. The tracheation of the nymphal wing-pads of Decticus verrucivorus

divides once more, these two branches forming the anterior and distal margins of the 'mirror' in the adult. Trachea Cu_2 runs parallel to Cu_1 and Cu_{1b} to the wing-margin in the female; in the male it diverges posteriorly forming the proximal margin of the mirror in the right wing-pad, and representing the adult stridulayory rib in the left wing-pad.

In all the wing-pads examined the first anal trachea was unbranched, running parallel to Cu and Cu_2. The remaining anals, of which there are usually one or two and rarely more than three, arise from a common stem.

(b) Hind wing-pad.

The costal and subcostal tracheae are of the usual Saltatorian type: the former is much shorter than the latter and they arise at the base from a short common stem. The radial trachea is similar to that of the fore wing-pad, though R_s usually bears fewer branches.

Trachea M, as in the fore wing-pad, gives rise to a very reduced posterior branch representing MP, which normally joins an anterior branch (Cu_{1a}) arising from Cu_1. The resultant trachea, when well-developed, gradually converges on to Cu_{1b}; it frequently gives rise to an anterior accessory branch, MP_a. The first and second cubital tracheae (Cu_1 and Cu_2) separate near the base of the wing-pad. Cu_{1b} and Cu_2 are strongly developed, but Cu_{1a} is a small trachea and is probably not always present.

The anal tracheae are typically Saltatorian, 1A having a separate origin from the remainder, which arise from a common

stem.

The above account of Tettigoniid tracheation applies to its most typical arrangement, but variations from this are frequent. As these differences are always reflected in the venation, they are discussed later when the adult veins are described.

3. THE VENATION OF THE ADULT WINGS

(a) The shape and areas of the wings.

(i) Fore wing.

Tettigoniid fore wings vary enormously in shape. This variation is largely the result of mimicry, leaf- and fruit-mimics generally having lobe-like fore wings and grass-stem-mimics having very elongate, narrow fore wings. The normal shape of the fore wing is probably similar to that of Tettigonia viridissima (see Fig. 44 ~~42~~).

One of the most remarkable shapes is shown by Acridoxena hewaniana Smith (see Fig. 43). The fore wings of Thliboscelus camellifolia Audinet-Serville ~~(see Fig. 44)~~ are inflated to form a balloon-like sheath from which only the head, pronotum, and legs, protrude (see Fig. 45). Those of Morsimus form a flatter scale-like covering.

In the male there is frequently a widening at the base of the fore wing to accommodate the stridulatory apparatus; examples of this are shown by Tympanophora (see Fig. 46), Prochilus (see Fig. 47), and Decticus verrucivorus (see Fig. 48).

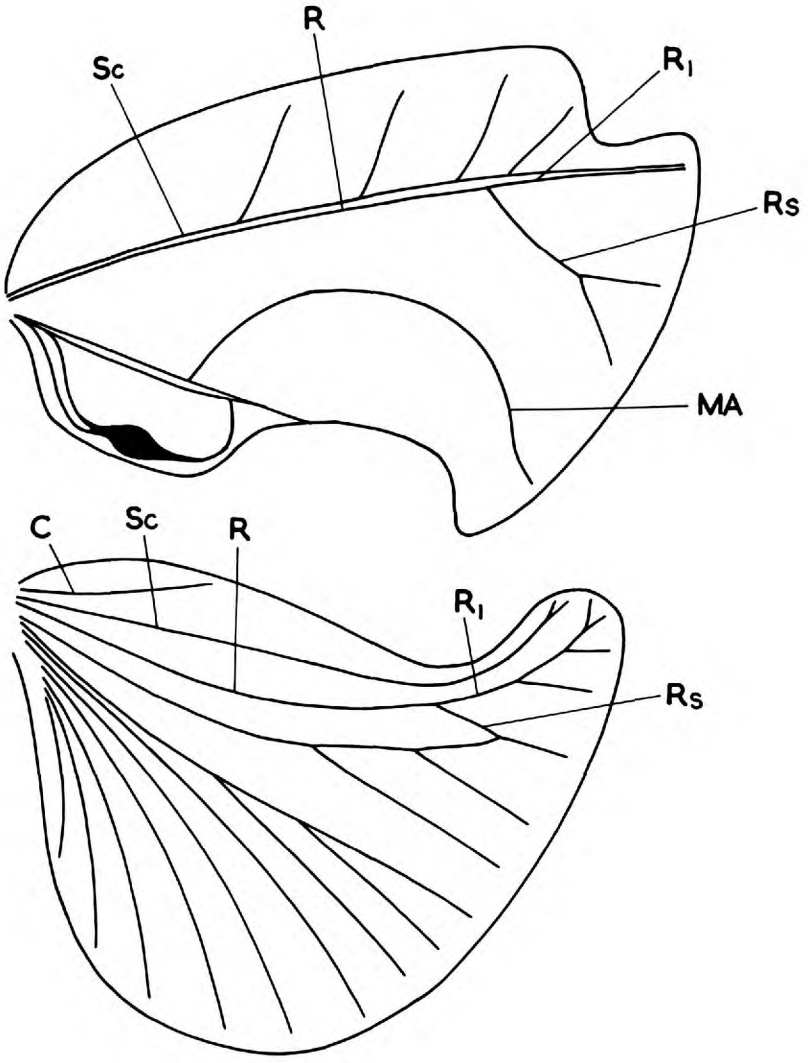
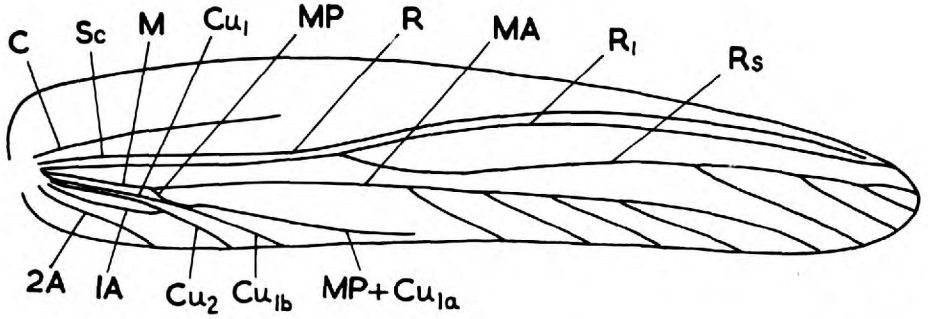
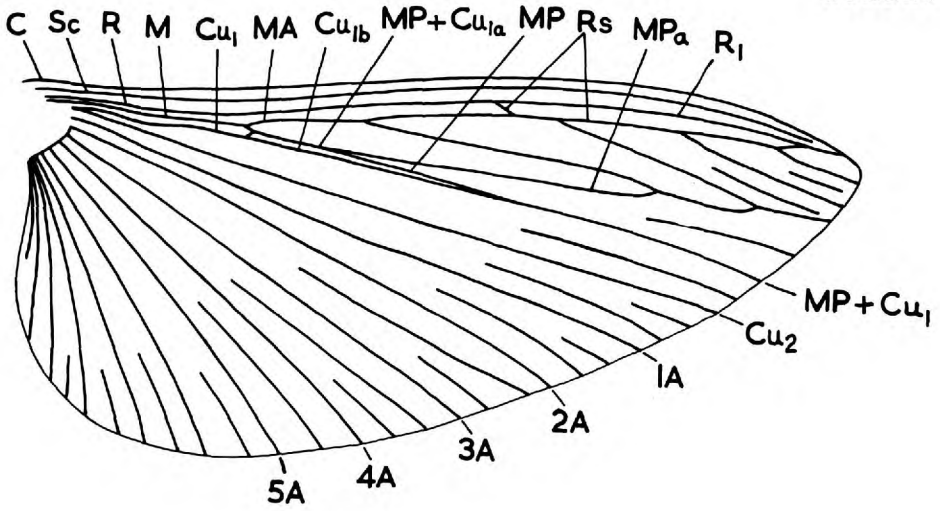
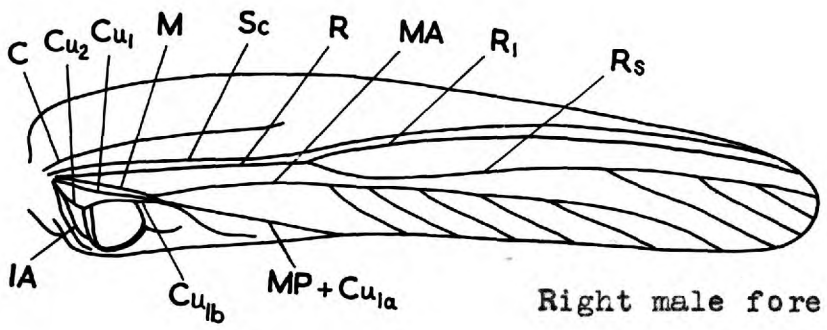


Fig.43. The right wings of Acridoxena hewaniana, male.

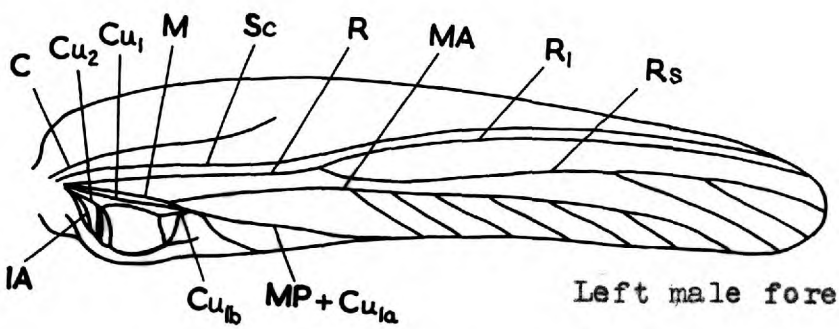


Female.





Right male fore wing.



Left male fore wing.

Fig.44. The wings of Tettigonia viridissima.

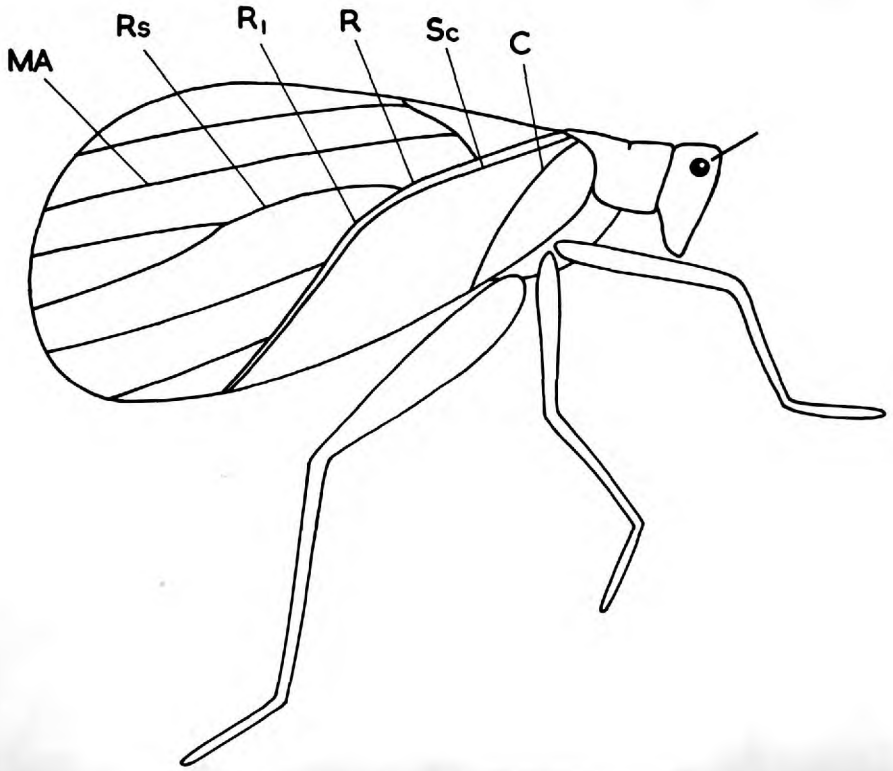


Fig.45. Diagrammatic lateral view of Thliboscelus camellifolia.

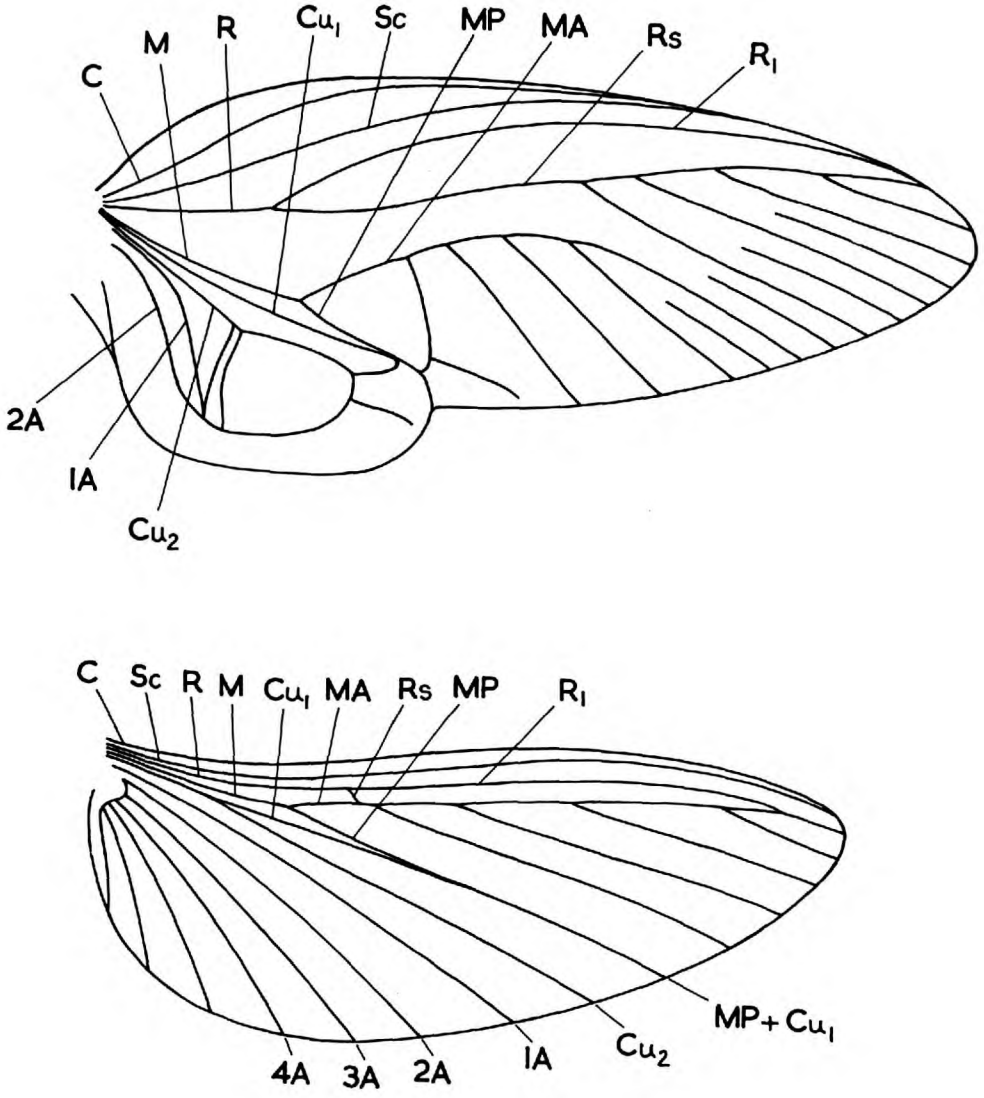


Fig.46. The right wings of Tympanophora uvarovi, male.

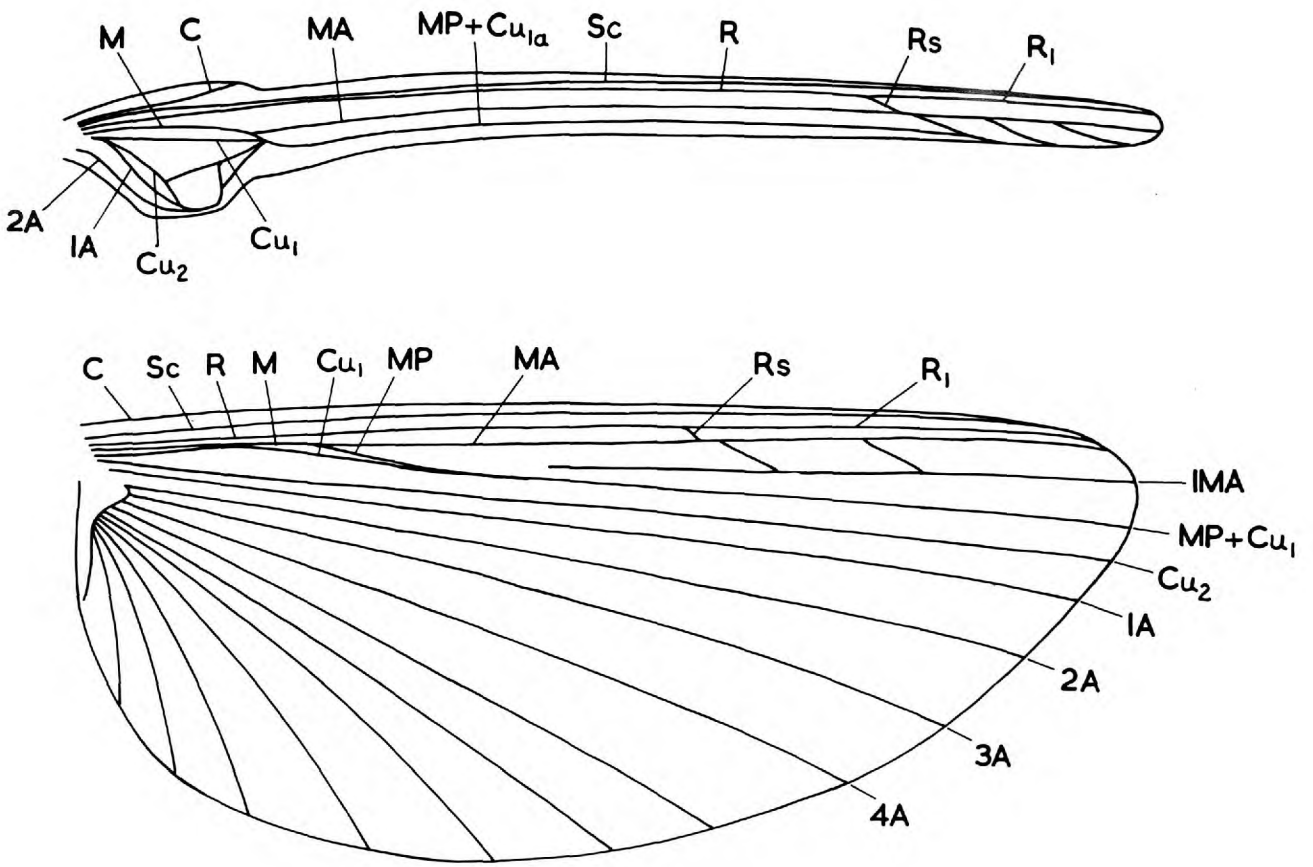


Fig.47. The wings of Prochilus australis, male.

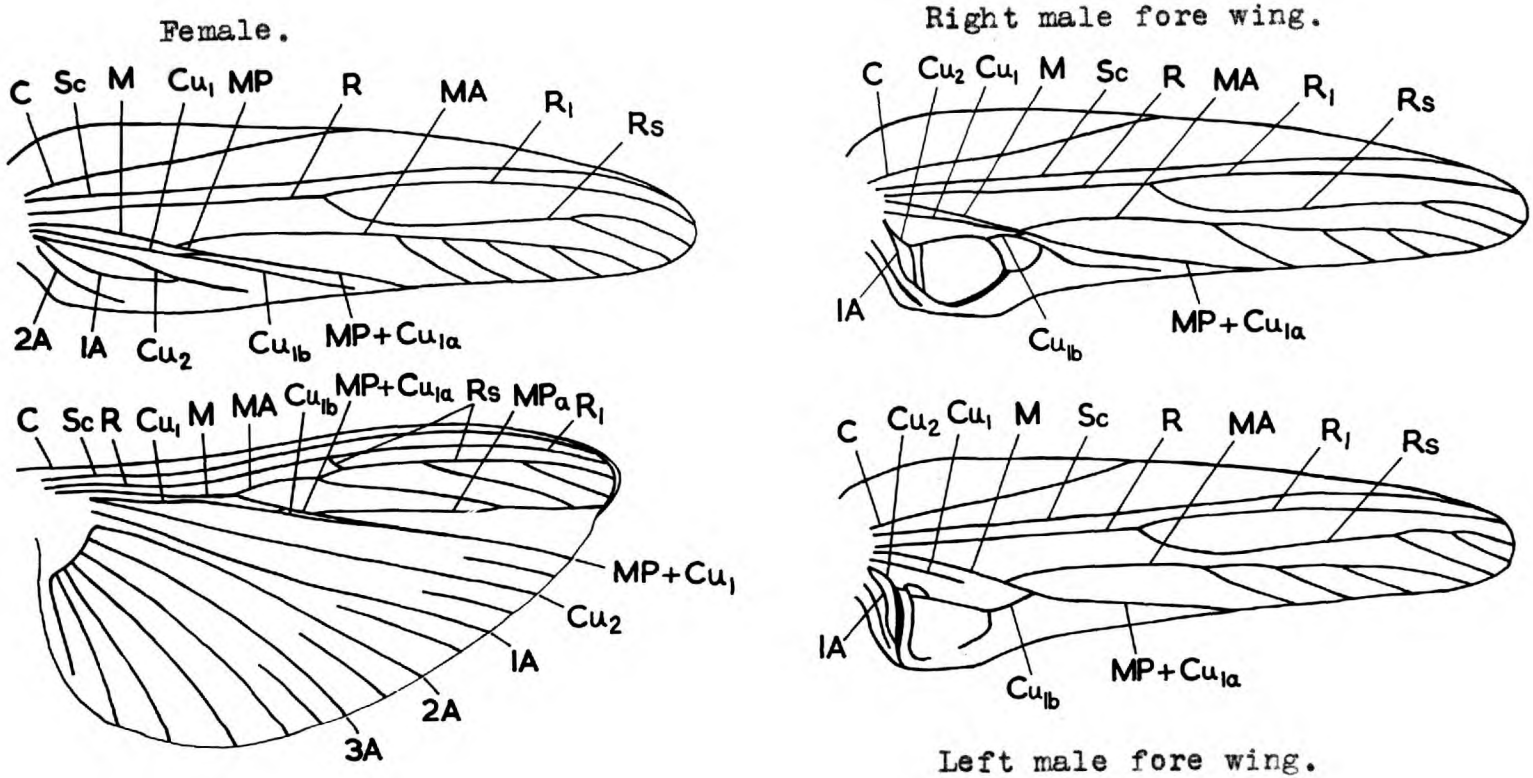


Fig.48. The wings of Decticus verrucivorus.

Apterous and brachypterous forms are common in the Tettigoniidae, as in other Saltatoria. The subfamilies Ephippigerinae, Pycnogastrinae (see Fig. 48a), Bradyporinae, Deracanthinae, and Hetrodinae, are always brachypterous or apterous.

The texture of the fore wings also varies a great deal. Frequently they are quite membranous (e.g. Mecopoda, Hexacentrus), but many of the leaf-mimics have fore wings of a rather leathery consistency (e.g. Corycus jurinei Saussure, female). In some cases the pronotum covers a small membranous area of the fore wings, the remainder being tougher in consistency; this is typical of the Phyllophorinae.

No attempt has so far been made to apply names based on the Comstock-Needham System to the areas of Tettigoniid wings. A proposed scheme is shown in Fig. 49.

(ii) Hind wing.

The typical shape of Tettigoniid hind wings is shown by those of Tettigonia (see Fig. ~~42~~ 44). A ~~cycloid~~ semi-circular shape, however, is typical of the subfamily Pseudophyllinae, group Acanthodini (sensu Zeuner, 1939, pp. 110 and 111) (e.g. Xerophyllopteryx, see Fig. 50).

The hind wings are usually of the same length as the fore wings, and elongation of the latter is normally accompanied by the same process in the hind wings (e.g. Clonia wahlbergi Stal, see Fig. 51; Prochilus australis Brulle, see Fig. 47). In the Phaneropterinae, however, the hind wings are typically longer than the fore wings (see Fig. 52).

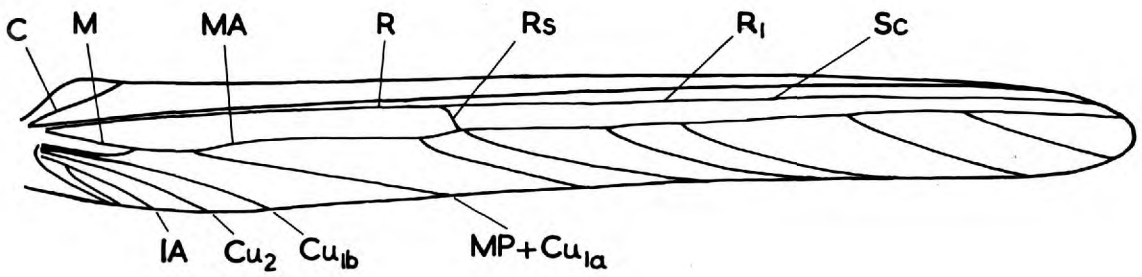
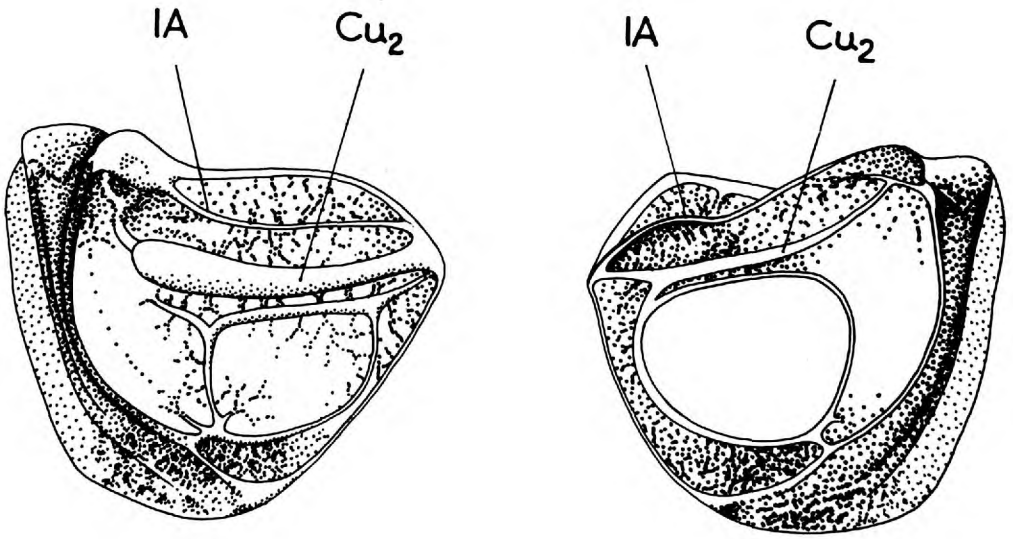


Fig.51. The fore wing of Clonia wahlbergi, female.



Left. Right.

Fig.48a. The fore wings of Pycnogaster, male.

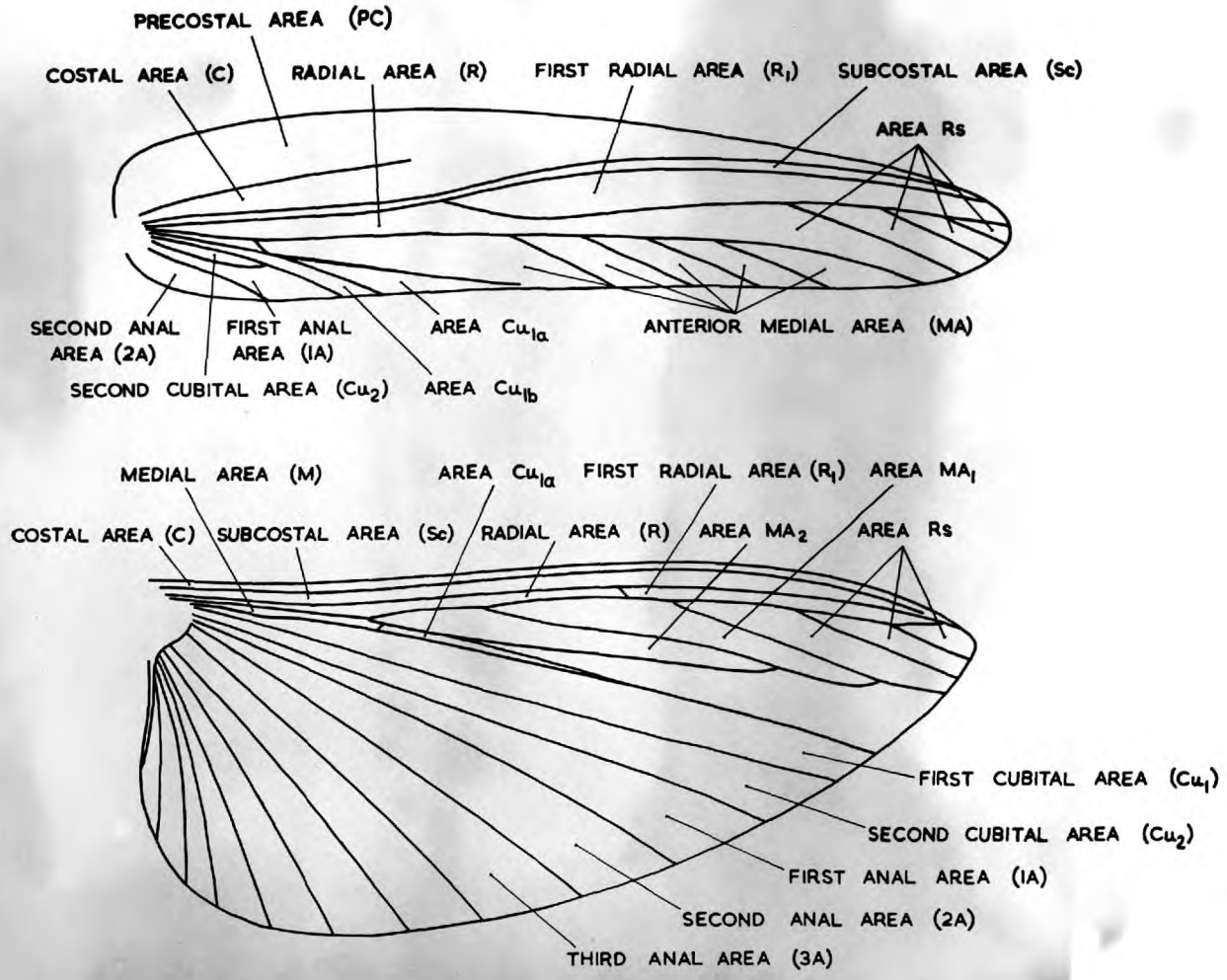


Fig.49. The areas of Tettigoniid wings.

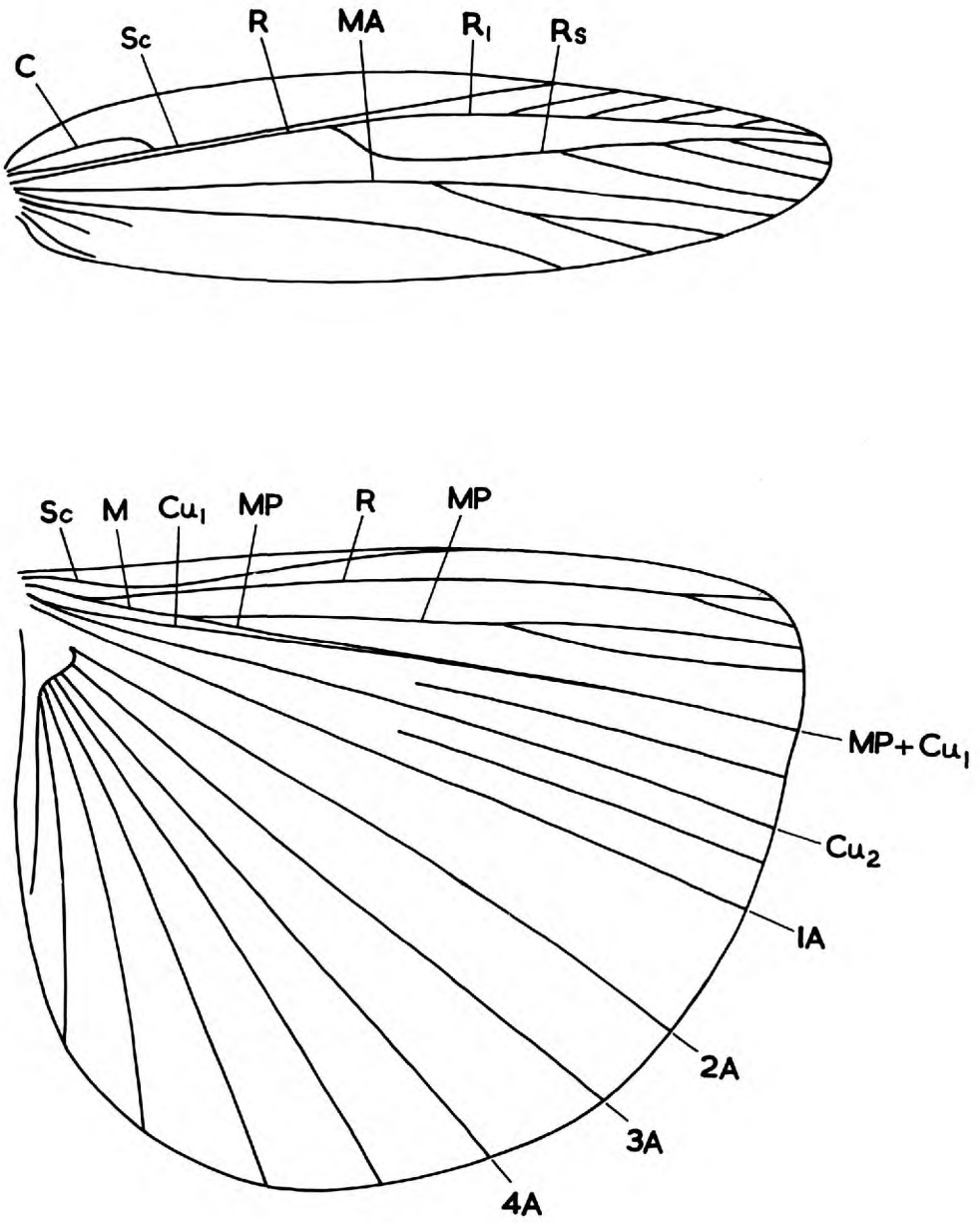
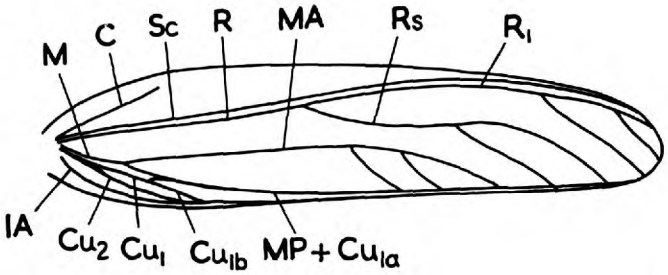
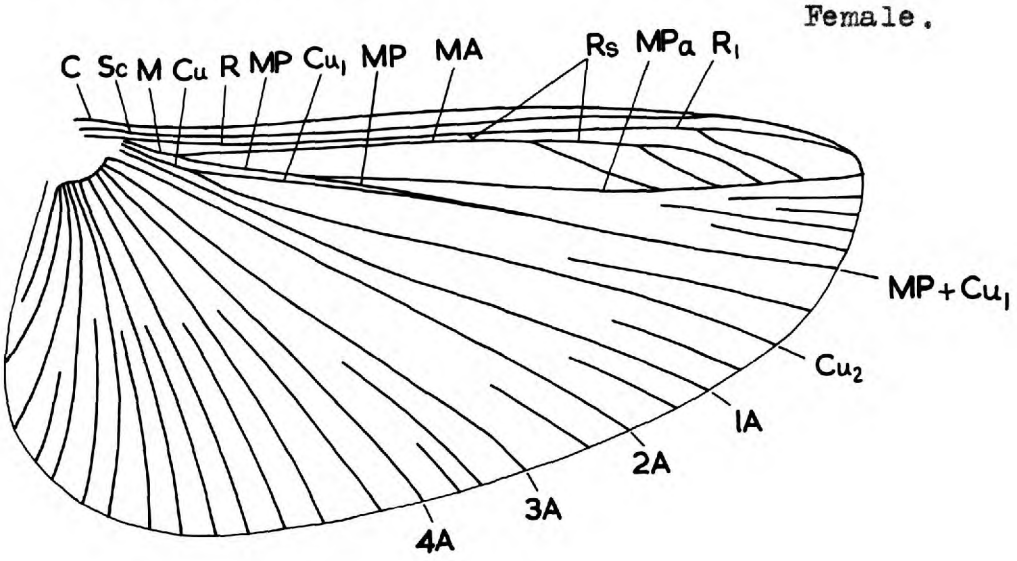
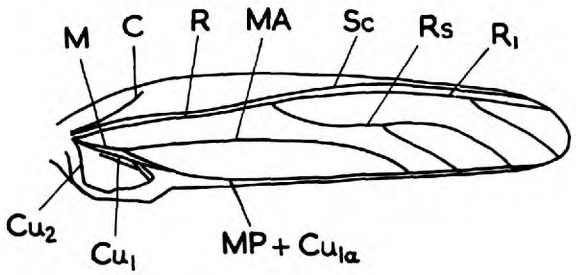


Fig.50. The wings of Xerophyllopteryx, female.

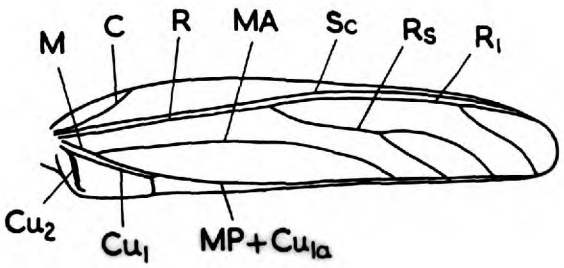


Female.





Right male fore wing.



Left male fore wing.

Fig.52. The wings of Phaneroptera quadripunctata Brunner.

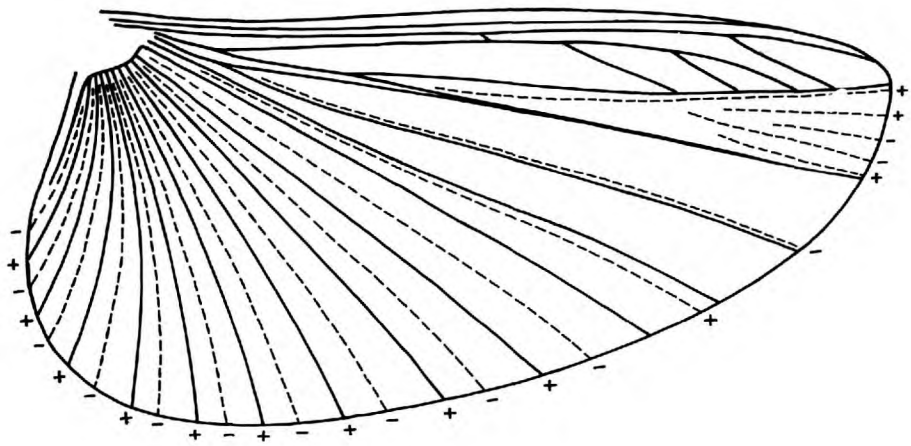


Fig.53. The folds in the hind wing of Phaneroptera quadripunctata.

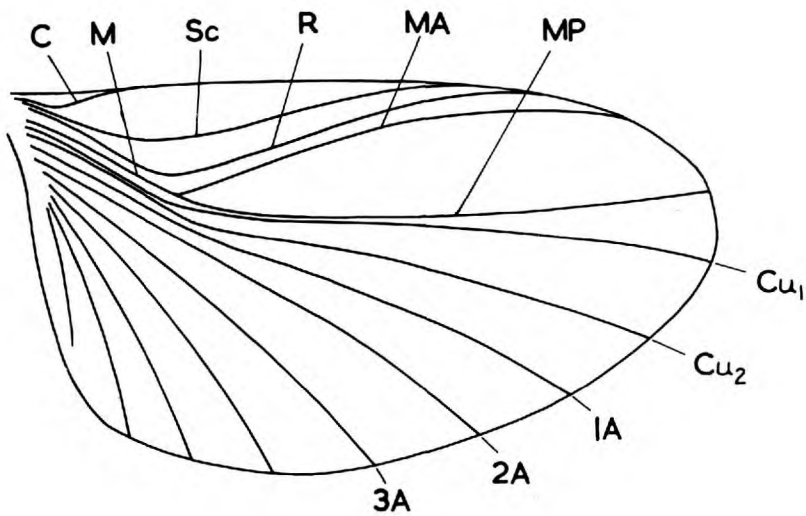


Fig.54e. The hind wing of Thliboscelus camellifolia.

The areas of a typical Tettigoniid hind wing are shown in Fig. 49.

(b) Folding.

The flexed fore wing is typically folded along a line of weakness between Cu_1 and Cu_2. This is an unusual position for a fore wing fold, there being usually a hinge in the region of 1A. In the male, which has a wider area between Cu_1 and Cu_2 in the fore wing, the fold lies just behind Cu_1.

The result of this fold, which may be called the cubital hinge, is to bring the area of the fore wing behind Cu_1 into a roughly horizontal position over the abdomen, the remainder of the wing being roughly vertical, as a rule. Although typical of the family, this folding is not always well-marked and has been largely lost in many leaf-mimics.

In the hind wing (see Fig. 53) the first fold occurs just behind MP_a. This fold is convex and is followed by a concave fold just anterior to Cu_2. The next fold is convex and lies just behind 1A. This is followed by a succession of concave folds alternating with the convex anal veins. There is often additional folding in the area between MP_a and $MP+Cu_1$ (area MP_a) near the wing-margin.

These folds enable the fan formed by the cubito-anal lobe of the hind wing to close neatly under the fore wing, when flexed.

(c) The wing-base.

At the base of each wing there is a flexible region

which enables it to be extended or flexed. This consists of an axillary membrane bearing a number of axillary sclerites which intermediate between the bases of the veins and the thorax.

La Greca (1947) has made a study of this region of Tettigoniid wings, examining representatives of the subfamilies Phaneropterinae, Copiphorinae, Tettigoniinae, and Decticinae. The account given below is largely based on Tettigonia viridissima (see Fig. 54) and confirms his main conclusions.

The base of each wing will be dealt with separately.

(i) Fore wing.

The first axillary is in the usual position, between the mesonotum and second axillary. Anteriorly it articulates with the fused bases of the costa and subcosta. There is a small tegula at the base of the costa.

The second axillary is a large sclerite, hinged on to the first axillary, and articulating laterally with the bases of the media and radius and posteriorly with the comparatively small third axillary. On the latter sclerite is inserted the flexor muscle of the wing.

The fourth axillary, usually either small or absent, is normally well-developed in the Tettigoniid fore wing. It is hinged with the mesonotum on one side and is connected with the third axillary and to some extent with the bases of the anal veins on the other.

The median plates are poorly developed in the Tettigoniid fore wing. They cannot be distinguished in Tettigonia, but

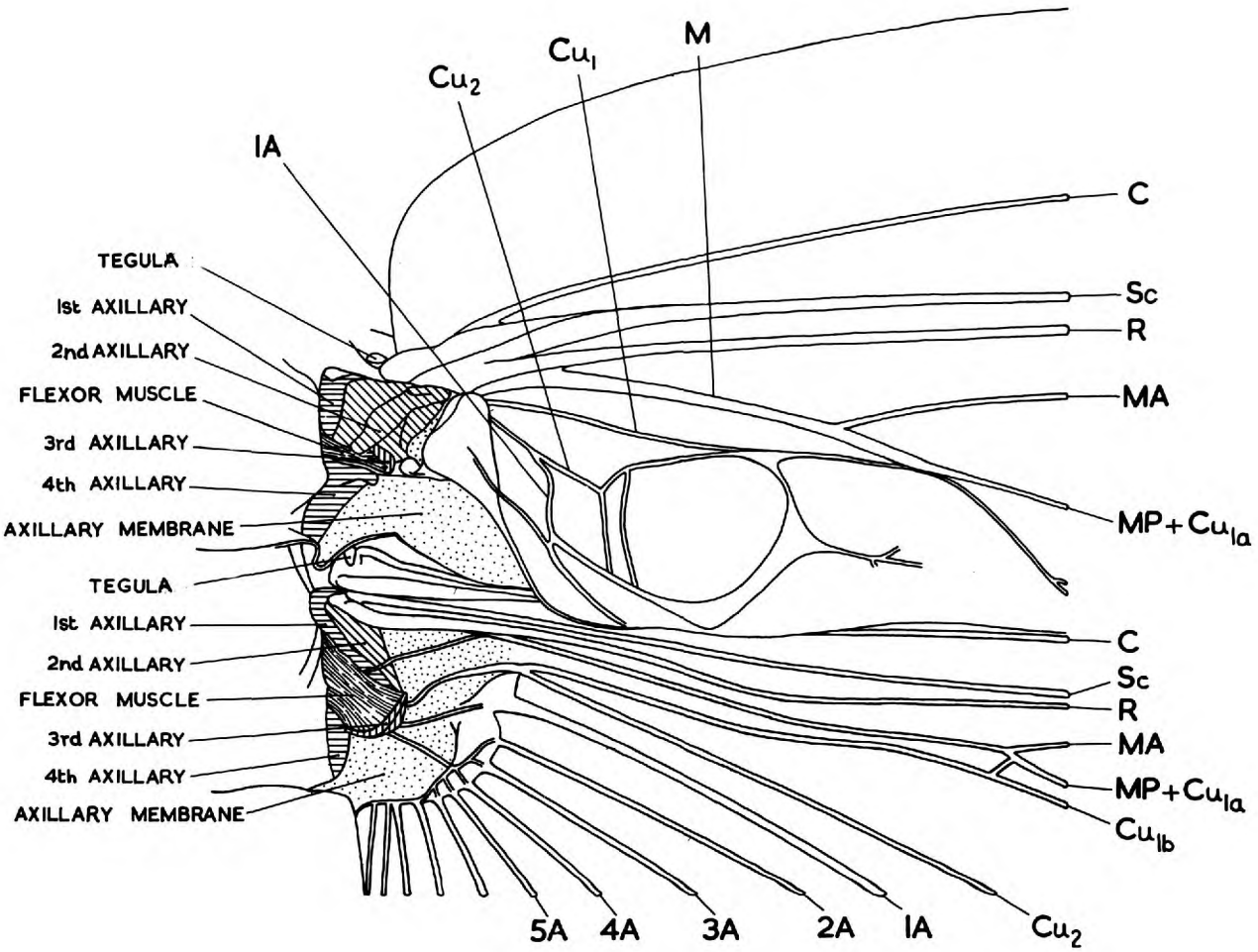


Fig.54. The right wing-bases of Tettigonia viridissima, male.

may sometimes be present as slight thickenings in the axillary membrane.

The posterior part of the fore wing-base consists of unsclerotized axillary membrane.

(ii) Hind wing.

The first axillary of the hind wing is in exactly the same position as in the fore wing, and there is a tegul~~um~~a at the base of the costa. The second axillary hinges proximally with the first axillary and has an anterior articulation with the base of the radius.

The third axillary is larger than in the fore wing, providing an insertion for the much larger flexor muscle. The fourth axillary, on the other hand, is rather smaller; it articulates distally with the third axillary.

As in the fore wing the median plates are very poorly developed; they are sometimes represented by slight thickenings in the axillary membrane.

(d) The veins.

The veins of Tettigoniid wings may be classified in the same way as those of the Pneumoridae, and the various types are defined under ~~this~~ that family (see p. 66 et seq.).

(i) The ambient veins.

Ambient veins are a common feature of Tettigoniid fore wings. There is usually a continuous vein running round the whole of the margin of the fore wing, becoming rather

feebly developed towards the base of the wing. The vein may be actually on the wing-margin, or a very short distance from it. In Tettigonia viridissima, for example, the ambient vein is on the margin along the more distal part of the leading edge of the fore wing, but a short distance from it elsewhere; in Sathrophyllia, on the other hand, the ambient vein lies along the margin throughout its length.

In the hind wing there is often no ambient vein. Sometimes, however, a short ambient vein is developed round the distal extremity of the wing, as a continuation of the costa. This is the case in Tettigonia, for example.

(ii) The longitudinal veins.

A. Primary veins.

THE COSTA (C)

In the Tettigoniid fore wing the costa is always submarginal and almost always poorly developed. It rarely reaches more than halfway along the wing, and is often very short. A typical costa is found in the fore wing of Tettigonia viridissima, in which it attains about a third of the length of the wing. In some forms the costa is absent in the fore wing (e.g. Narea compacta Walker, Mioacris exaltatus (Walker)). Only in the males of the subfamily Tympanophorinae (see Fig. 46) is a strongly developed costa found in the fore wing.

The tip of the costa usually bends towards the anterior margin of the fore wing, meeting it at an angle (when reaching

it at all), but it joins it asymptotically in the Tympanophorinae; sometimes it bends back to join the subcosta (e.g. Xerophyllopteryx).

In the hind wing the costa is almost invariably well-developed, running along the anterior margin. Some exceptions to this are Simodera acutifolia Brunner, in which it is poorly developed, Lesina blanchardi Brongniart, in which it is very feebly developed, Salomona pupus Pictet and Acridoxena hewaniana, in which it is both poorly developed and submarginal, and Xerophyllopteryx, in which it is absent.

The costa is always unbranched in the hind wing, but often bears anterior accessory branches in the fore wing (e.g. Tettigonia). It is often slightly convex in the fore wing and nearly always strongly so in the hind wing.

THE SUBCOSTA (Sc)

This vein is always well-developed in fully winged species. In the fore wing it usually takes the form of a very gentle sigmoid curve, reaching the anterior margin at or near the tip of the wing. In many of the leaf-mimics, however, it is curved up towards the anterior margin rather sooner than usual, taking on the appearance of a lateral leaf-vein (e.g. Cycloptera speculata Brunner, Fig. 54 b), and in Tympanophora it reaches the margin close to the point at which the costa does.

The subcosta is usually some distance behind the anterior margin in the fore wing; sometimes nearly half the wing-area is in front of it. In some forms, however, the

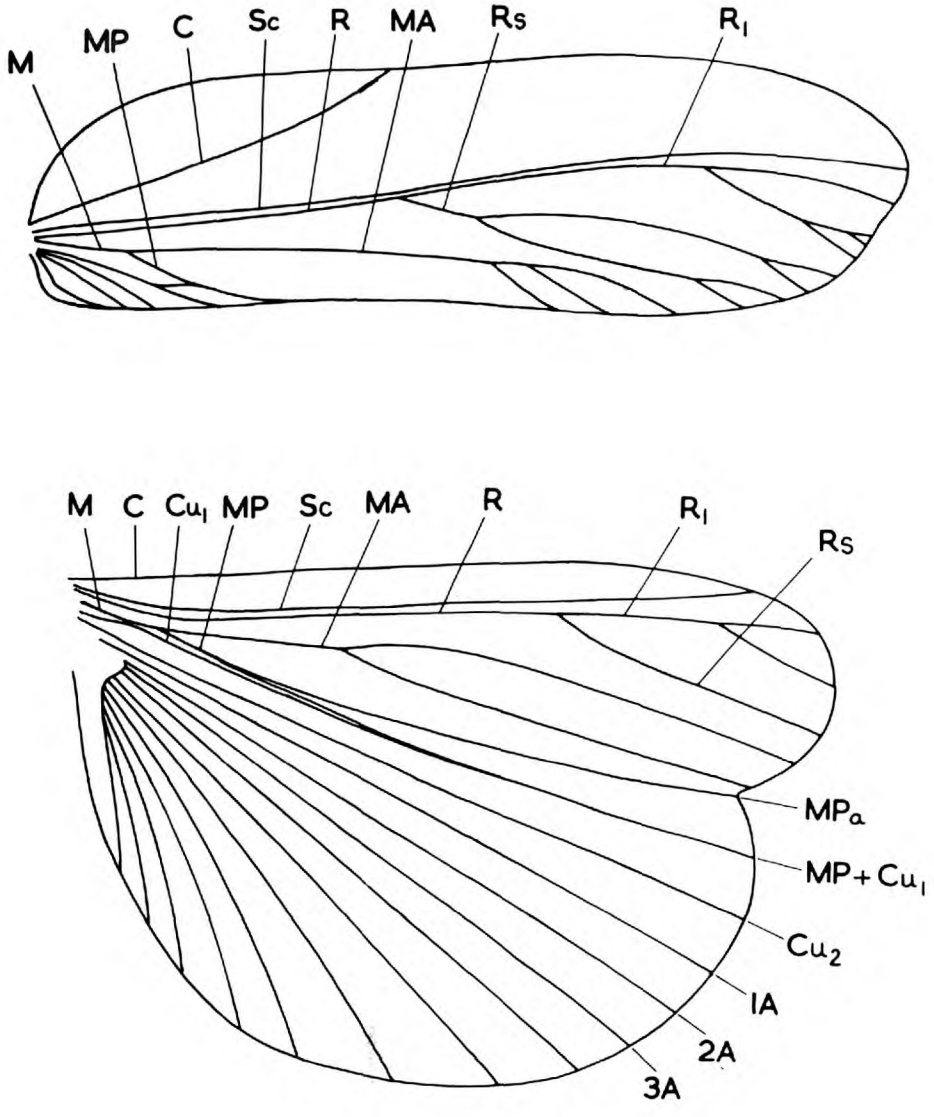


Fig.54a. The wings of Lesina Blanchardi, female.

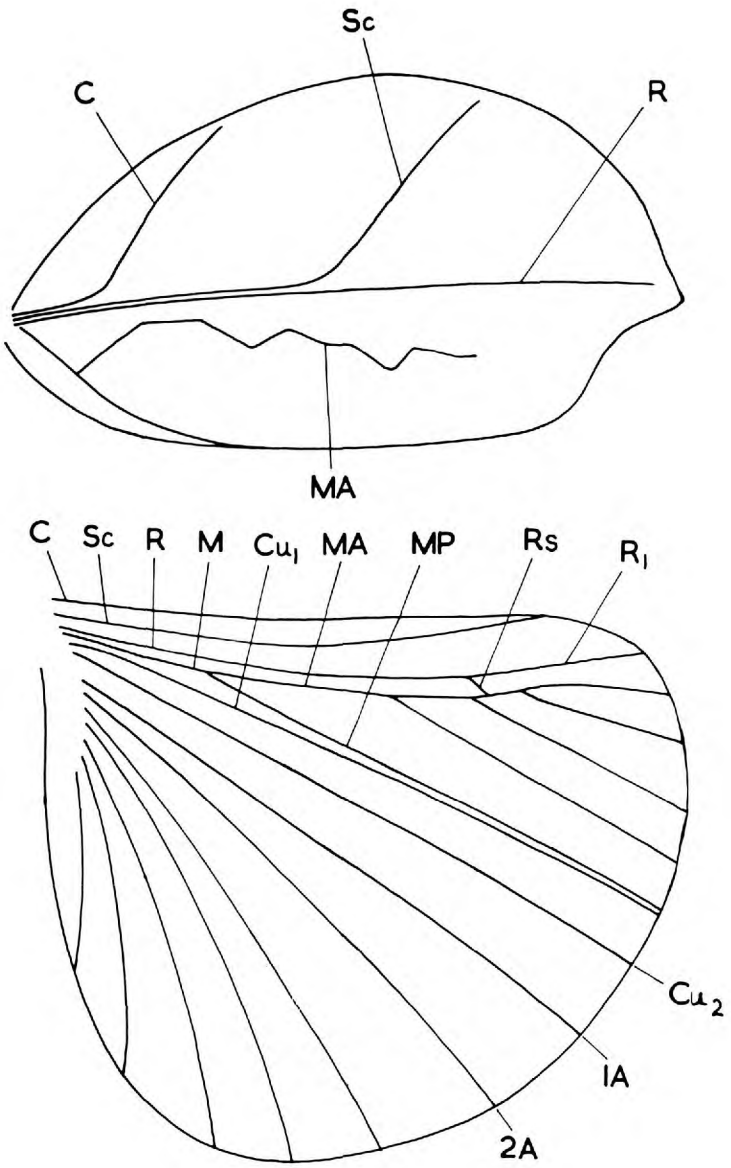


Fig.54b. The wings of Cycloptera speculata, female.

costal and precostal areas are small (e.g. Clonia, Prochilus, Tympanophora). There are often a number of subcostal accessory branches in the costal area (e.g. Tettigonia, Hexacentrus (Fig. 54c and d)).

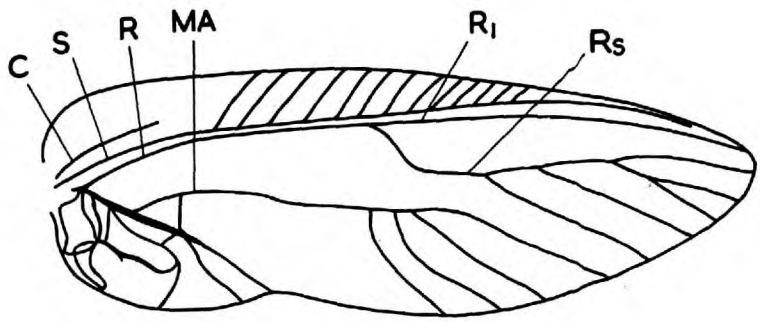
In the hind wing the subcosta normally runs parallel to the costa and a short distance behind it. The costal area is rather larger than usual in some forms (e.g. Thliboscelus camellifolia (Fig. 54e), Narea compacta, Simodera acutifolia). The subcosta does not normally touch the anterior margin in the hind wing; an exception to this is Xerophyllopteryx, in which it reaches it about halfway along its length.

The costal area is almost invariably supported only by cross-veins, but in Lesina blanchardi accessory subcostal branches are developed in it.

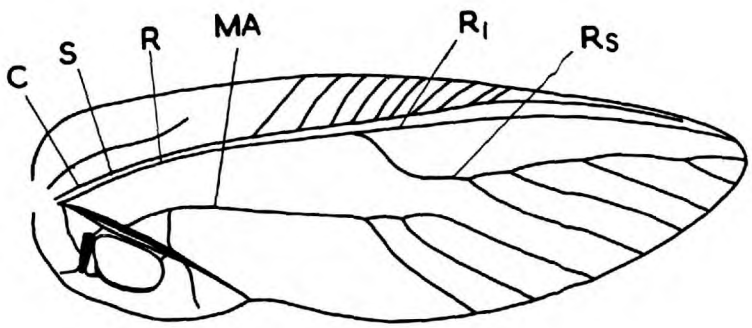
The subcosta is typically concave in the fore wing and almost invariably so in the hind wing.

THE RADIUS (R)

The radius is situated immediately behind the subcosta in both pairs of wings. The space between these two veins (the subcostal area) is normally the same width as the costal area in the hind wing, but varies a great deal in the fore wing. In the fore wings of Phyllophora (Fig. 54f), for example, Sc and R are closely approximated; this is often the case with leaf-mimics. In Sathrophyllia (Fig. 54g) there is an extremely small subcostal area in the fore wing; Homorocoryphus (Fig. 54h) and Mecopoda (Fig. 54i) show a progressively larger one. In Tettigonia viridissima the subcostal area is of typical size, and has a slight constriction in the region where the radius bifurcates - a common feature in the family.



Right.



Left.

Fig.54c. The male fore wings of Hexacentrus.

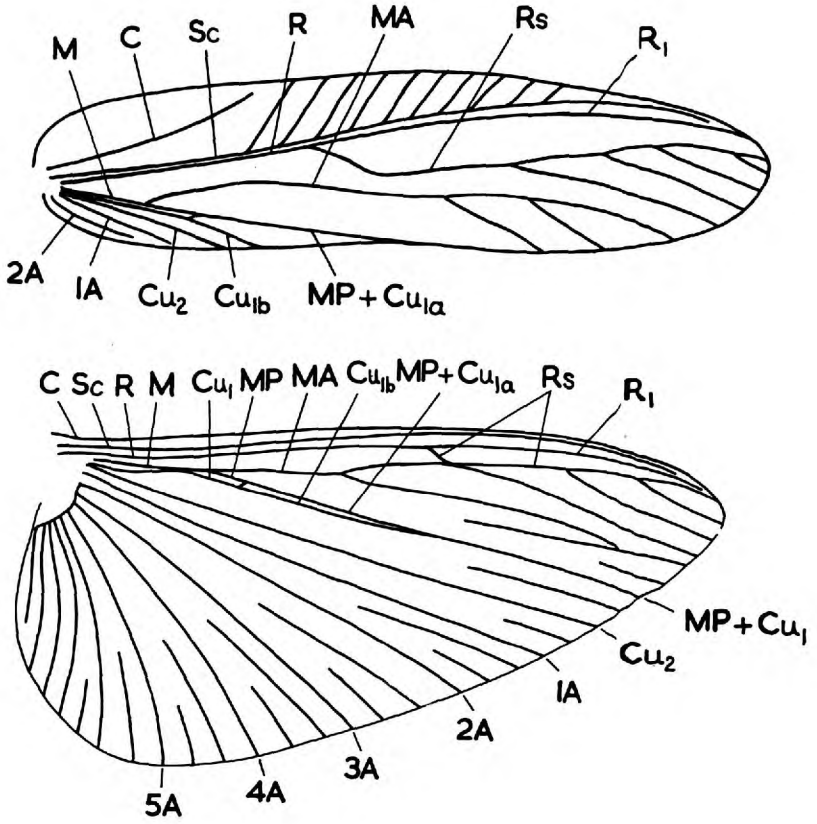
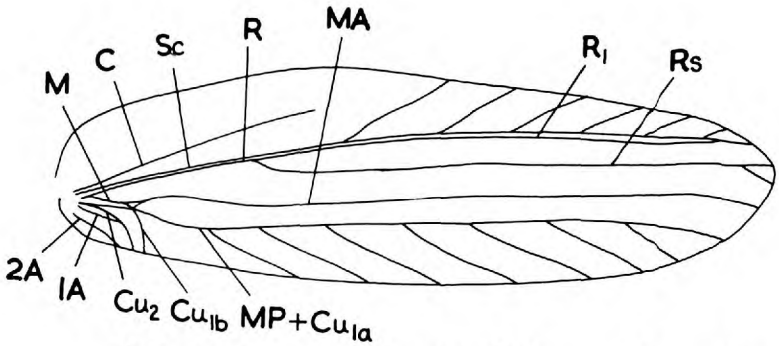
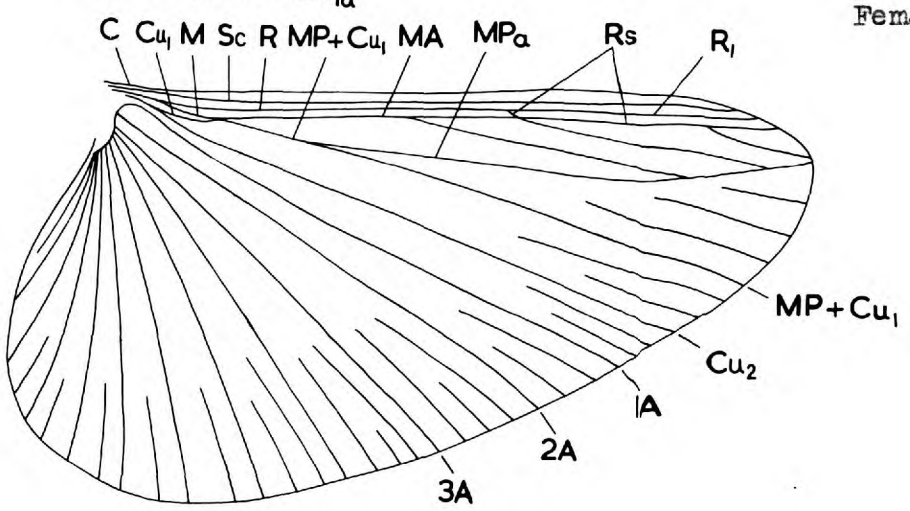
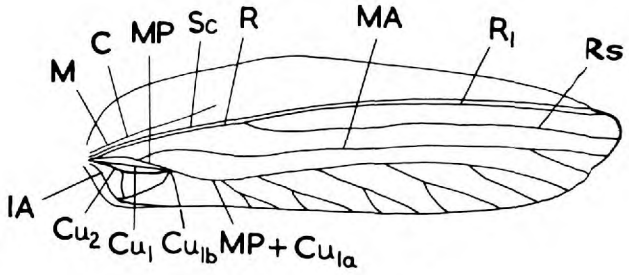


Fig.54d. The wings of Hexacentrus, female.

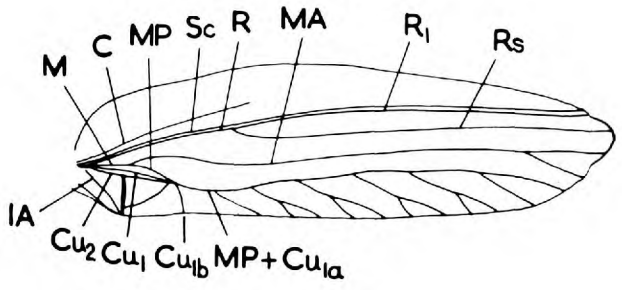




Female.



Right male fore wing.



Left male fore wing.

Fig.54g. The wings of Sathrophyllia.

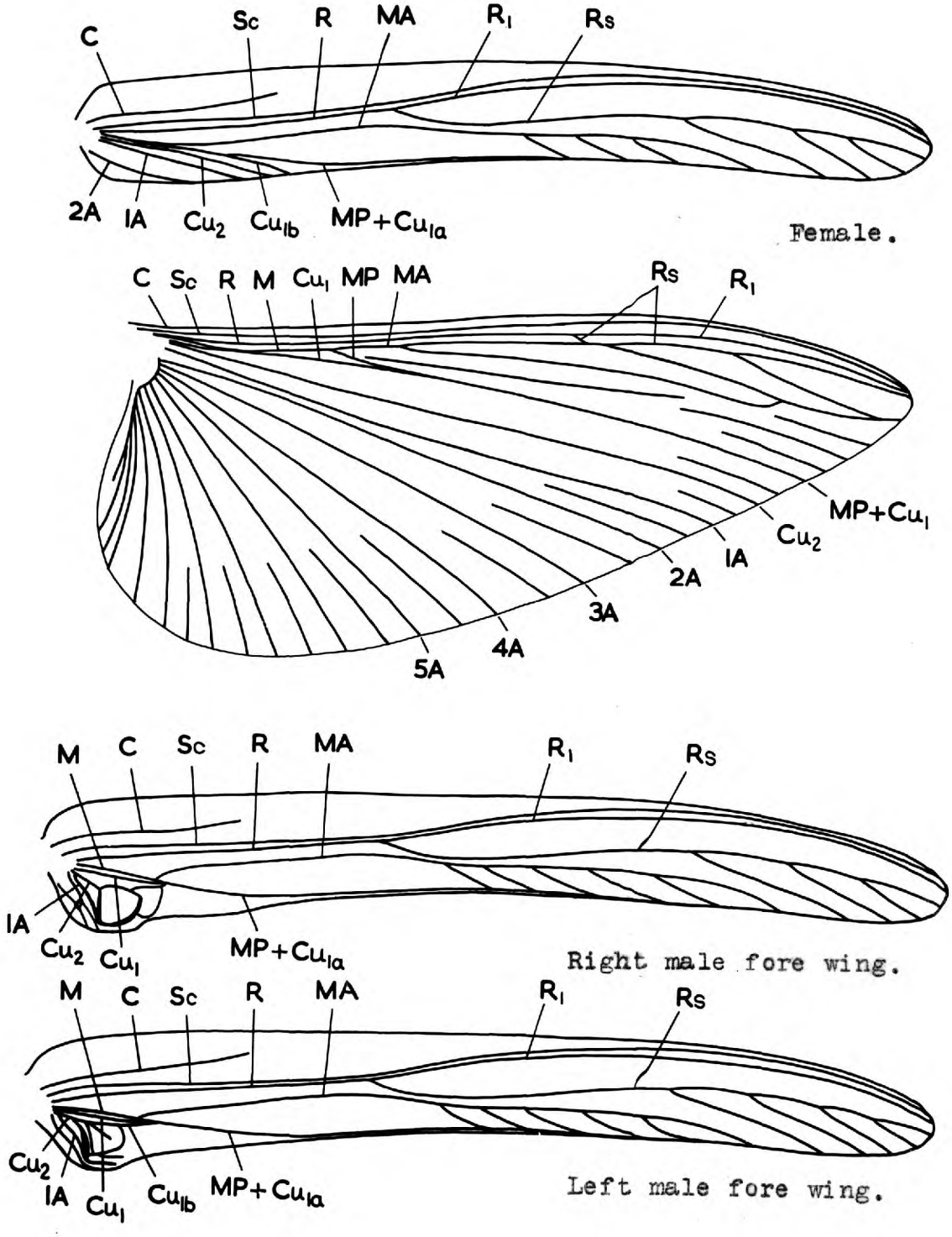
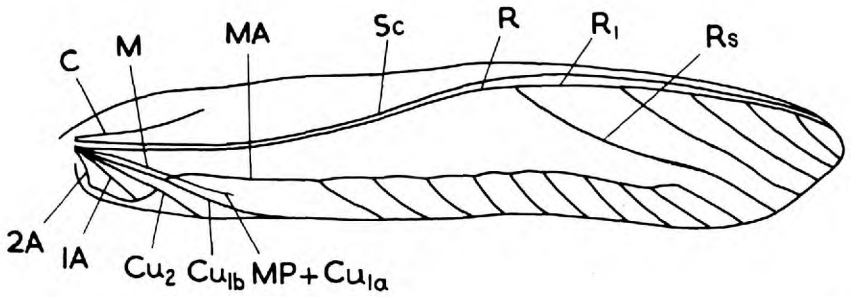
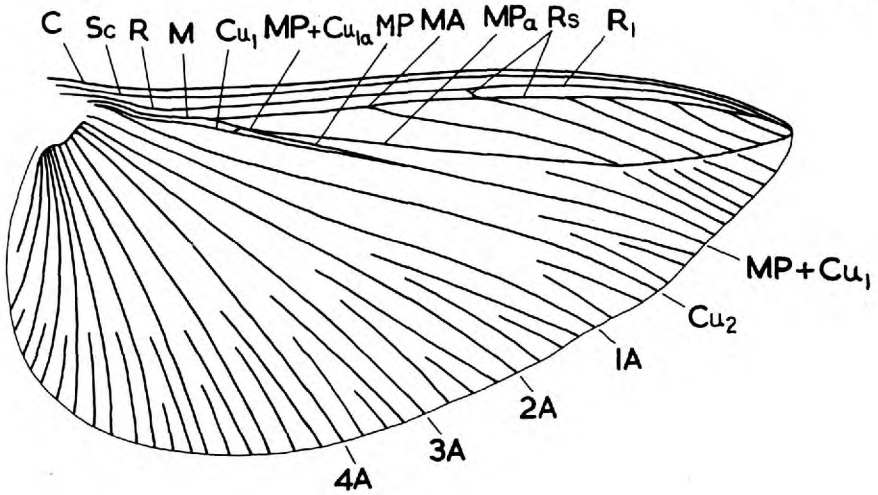
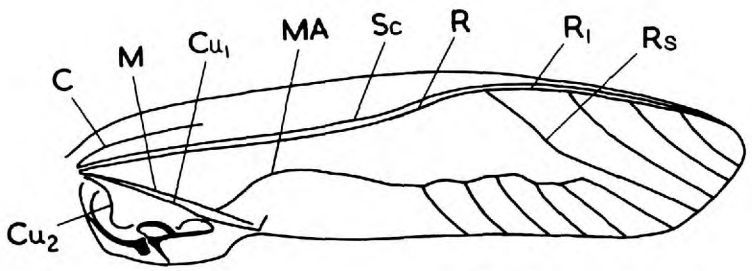


Fig.54h. The wings of Homorocoryphus vicinus.

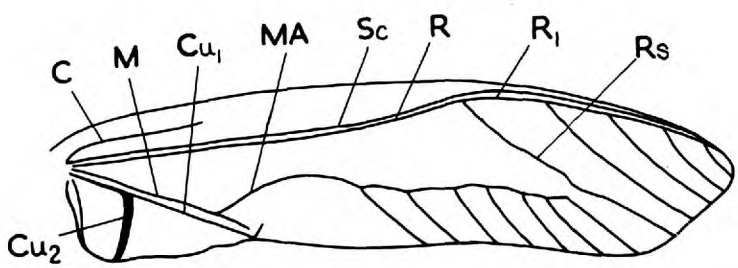


Female.





Right male fore wing.



Left male fore wing.

Fig.54i. The wings of Mecopoda elongata (Linnaeus).

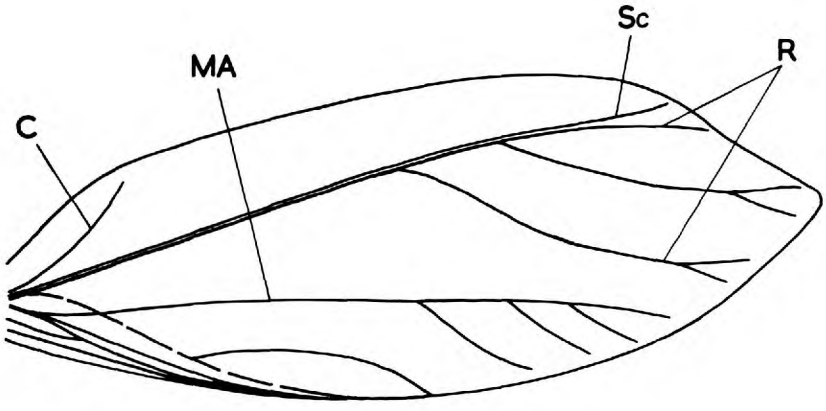


Fig.54f. The fore wing of Phyllophora.

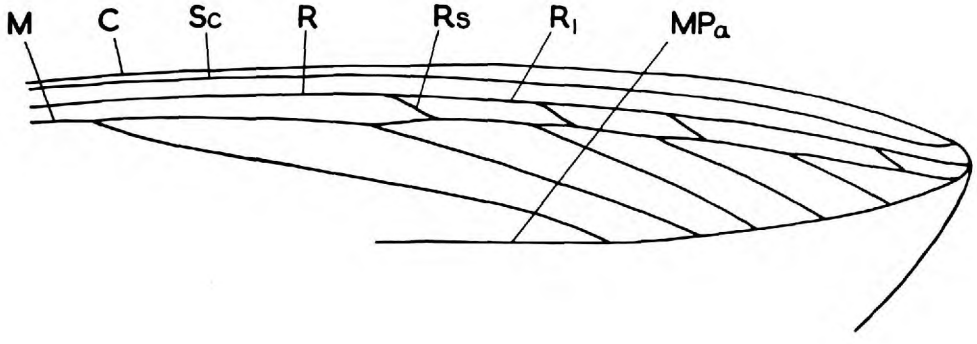


Fig.55. Part of the hind wing of Phyllophorella woodfordi.

The radius almost invariably becomes divided into R_1, which is usually unbranched, and a pectinately branched radial sector (R_s). In the fore wing this division usually occurs in the proximal half of the wing in the more generalized members of the family, but is about halfway along it in Hexacentrus (male), Lesina blanchardi (Fig. 54a), and Mioacris exaltatus, and is in the distal half in Acridoxena hewaniana, Diophanes, Tympanoptera, and Chlorobalius, for example. The radial sector is sometimes absent in the fore wings of leaf-mimics (e.g. Cyclopteryx speculata, Narea compacta, Simodera acutifolia). In the hind wing the bifurcation of the radius is almost always in the distal half of the wing. The radial sector is rarely absent in the hind wing (e.g. Thliboscelus camellifolia, Simodera acutifolia).

R_s is almost always free in the fore wing, but in some forms with narrow wings it has fused for part of its length with MA (e.g. Clonia, Prochilus, Chlorobalius). There is also a tendency for this to happen in the Copiphorinae. Occasionly the main stem of the radial sector becomes fused to R_1 (e.g. Pachysmopoda abbreviata Taschenberg). In the hind wing R_s is almost invariably fused for a short length to MA or one of its branches. Exceptions to this are Lesina blanchardi and Xerophyllopteryx, in which these two veins are completely free. The main stem of R_s takes the form of an oblique cross-vein before fusing with MA. In some large hind wings there are more than one of these oblique cross-veins; a good example of

this may be seen in the hind wings of some species of *Phyllophorella* (in *P. woodfordi* (Kirby), for example, there are three or four of these oblique cross-veins - see Fig. 55). They may be looked upon either as branches of R_1 or as branches of R_s arising from R_1+R_s.

R_1 is usually unbranched, but a branched R_1 is found in a number of forms, including *Lesina blanchardi*, *Salomona pupus*, and many of the Phaneropterinae. In these forms the branches are directed towards the posterior margin, but in the fore wings of *Xerophylloptery*x R_1 has anterior accessory branches, so that the radius is of the type characteristic of the Prophalangopsidae.

The radial sector is normally branched in a pectinate fashion, the number of branches varying a great deal but usually being less than six; the number is not constant for any particular species. In many of the leaf-mimics the radial sector is unbranched (e.g. *Mioacris exaltatus*, *Climacoptera*, *Corycus jurinei*) in the fore wing. There are often fewer R_s branches in the hind wing than in the fore wing.

The main stem of the radius is usually strongly convex in both pairs of wings. R_1 is also often convex, but R_s shows no definite tendencies in this respect.

THE MEDIA (M)

The form of this vein differs considerably in the fore and hind wings, and the two cases are therefore treated

separately.

Fore wing.

In the fore wing the media is situated a short distance behind the radius. It divides into two branches, MA and MP, near the base of the wing, the length of the main stem of the media generally being less than a sixth of the total wing-length. MA usually extends to near the tip of the wing whereas MP (which is often rather poorly developed in the female) generally fuses with Cu_{1a} and often reaches the posterior wing-margin in the proximal half of the wing. Sometimes MP (or MP+Cu_{1a}) is much longer than this, almost reaching the wing-tip; this condition is found, for example, in Prochilus, and in many Phaneropterines and Pseudophyllines.

MA typically bears a number of posterior accessory branches, though this is not invariably the case, especially when MP (or MP+Cu_{1a}) is well-developed. MP (or MP+Cu_{1a}) is usually unbranched, but when extended along the whole of the wing it often bears posterior accessory branches (e.g. many Pseudophyllines).

The main stem of the media is often convex; a tendency towards this condition is sometimes shown by MP, but MA is generally neutral in this respect.

Hind wing.

The space between R and M (the radial area) is usually about the same width as the costal and subcostal areas. The media bifurcates near the base of the wing into MA and MP; the former is generally better-developed than the latter. MA

usually divides again at least once in to MA_1 and MA_2; as already mentioned MA_1 almost invariably fuses for a short distance with R_s. The medial branches rarely reach the wing-margin; they join on to MP_a, an anterior accessory vein arising from MP (e.g. Phaneropterinae, Mecopodinae), or occasionally IMA, an intercalary vein developed in the anterior medial area (e.g. Prochilus australis). Examples of MA and MP reaching the wing-margin are shown by Salomona pupus, Cycloptera speculata, Tympanophora. In forms with reduced venation MA is sometimes unbranched in the hind wing (e.g. Simodera acutifolia).

The posterior media (MP) becomes closely applied to or (more usually) fused to Cu_1 shortly after leaving the main stem of the media. Before this fusion takes place MP is usually joined by a rather weakly developed anterior accessory branch (Cu_{1a}) arising from Cu_1; the free part of MP is therefore very short as a rule, the vein becoming $MP+Cu_{1a}$ and then $MP+Cu_1$. The free part of Cu_{1a} normally appears in the adult merely as an oblique cross-vein.

An accessory vein (MP_a) usually arises from MP or $MP+Cu_{1a}$, and often extends to the tip of the wing. The development of this vein is associated with the first anal fold of the hind wing, which runs just behind it. In Thliboscelus camellifolia MP_a does not extend to the wing-tip, but rejoins MP. MP_a is absent in Salomona pupus, Acridoxena hewaniana,

Cycloptera speculata, Simodera acutifolia, Tympanophora, Xerophyllopteryx, and many other forms.

The main stem of the media tends to be concave in the hind wing; MA shows no definite tendencies in this respect, but MP+Cu_{1a} is often convex.

During this account the terms anterior media and posterior media have been used in the Lameerian sense (Lameere, 1922). As has been discussed in Section VI (p. 46 et seq.), the Tettigoniid wing-venation can be easily derived from Protorthopteran forms such as Permacridites, via Hagla, Zalmona, and Termitidium, and nowhere on this evolutionary line is there any reason to suppose that either MA or MP has been lost.

THE CUBITUS (Cu)

As with the media the cubitus has a rather different form in the fore wing to that in the hind wing, and the two will therefore be dealt with separately.

Fore wing.

The cubitus divides at the base of the wing into Cu_1 and Cu_2. Cu_1 is situated immediately behind the media; it soon divides into Cu_{1a} and Cu_{1b}, the former of which fuses with MP. In the female Cu_{1b} runs straight to the wing-margin, just behind Cu_{1a}, but in the male it is normally bent back sharply towards the base of the wing and divides again forming the anterior and distal margins of the mirror in the right wing or its equivalent in the left wing.

Cu_2 lies just behind the cubital hinge in the female, and runs straight to the margin. In the male, however, it is

bent in a posterior direction, forming the stridulatory rib in the left wing and the proximal border of the mirror in the right wing.

Hind wing.

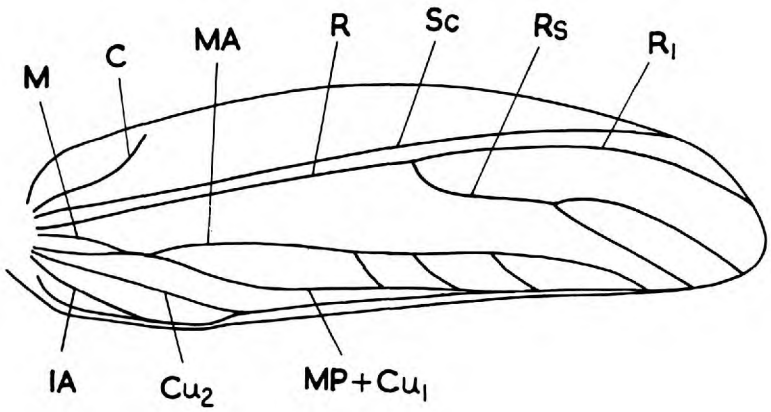
As in the fore wing the cubitus is divided from the base into Cu_1 and Cu_2. There is a tendency in some hind wings for Cu_1 to become fused to the main stem of the media for a short distance near the base of the wing; this has happened with Homorocoryphus and Meconema thalassinum (Fabricius) (Fig. 55a), for example, and the two veins touch in several forms (e.g. Platycleis).

Cu_1 usually divides into Cu_{1a} and Cu_{1b}; the former immediately fuses with MP and the latter generally does likewise more distally. Cu_2 is a straight unbranched vein, usually rather weakly developed at its base.

Cu_1 shows no definite convexity or concavity, but Cu_2 tends to be concave towards its base.

THE ANALS

In the fore wing there are generally two anal veins (1A and 2A). In the female they are normally straight and parallel, but in the male the courses of these veins are rather sinuous and much shorter, due to the presence of the stridulatory apparatus. Sometimes a third anal vein is developed (e.g. Hexacentrus, female). 1A generally becomes fused to Cu_2 in some forms (e.g Tettigonia). In leaf-mimics the anal area of the fore wing is often much reduced (e.g. Sathrophyllia, Cycloptera, Simodera, Phyllophora).



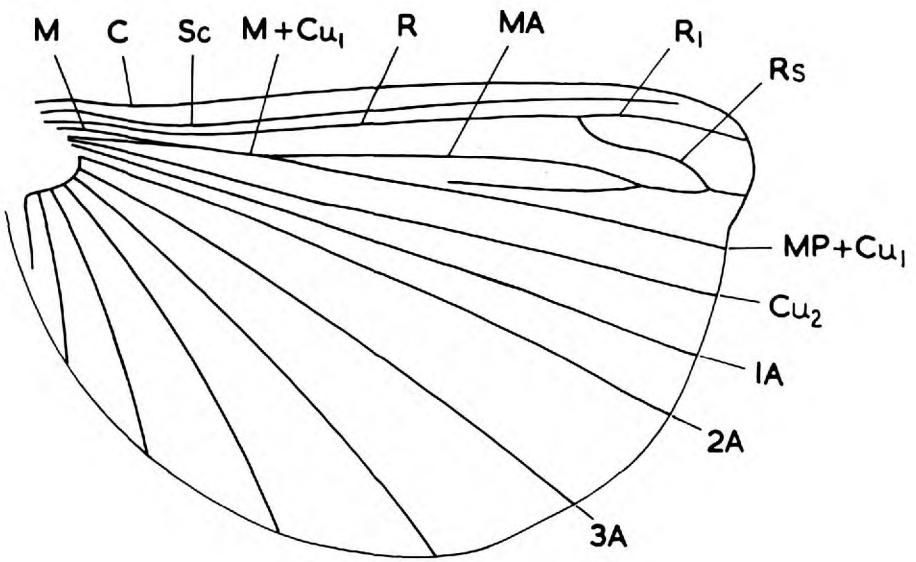


Fig.55a. The wings of Meconema thalassinum, female.

In the hind wing the development of the cubito-anal lobe has caused a considerable proliferation of veins in the anal area. There is little doubt that the strongly developed vein running posterior and parallel to Cu_2 is the first anal vein (1A), but it is impossible to be definite about the homologies of the remaining veins in the anal area (see pp. 45 and 28), of which there are generally between six and twelve.

B. Secondary veins.

Intercalary veins.

In Tettigoniid fore wings the spaces between the primary veins and their branches are filled with archedictyon and cross-veins: no intercalary veins are normally developed. The only fore wings examined which showed definite intercalary veins were those of Tympanophora uvarovi Zeuner, in which they are developed between some of the branches of R_s and MA. In another species of the same genus, T. pellucida White, they are not found.

In the hind wings intercalary veins are quite common, being largely associated with the folding of the cubito-anal lobe. The most anterior of them occur in area MA_2. Occasionally MP_a is replaced by an intercalary vein, IMA_2; examples of this are shown by Homorocoryphus vicinus (Walker), Copiphora cultricornis Pictet, and Prochilus australis. There ~~are~~ is often a number of small intercalary veins in the area MP_a. Intercalary veins are very frquently developed between the branches of the

cubitus and between the anal veins.

Accessory veins.

These veins are exceedingly common in Tettigoniid fore wings, due to some extent, no doubt, to the prevalence of leaf-imitation in the family. The costa often has accessory branches, and they are a common feature of the subcosta. The cross-veins between R_1 and R_s are often very oblique in the fore wing, and could in these cases be looked upon as accessory branches of R_1. R_1 sometimes gives rise to accessory branches of a more definite nature at its distal extremity, as, for example, in Lesina blanchardi, Tetraconcha fenestrata Karsch, Salomona pupus, Xerophyllopteryx, and many Phaneropterines.

Accessory branches are again a very common feature of MA in the fore wing, and MP (or $MP+Cu_{1a}$), when well-developed, frequently bears posterior accessory branches (e.g. many Pseudophyllines).

In the hind wing accessory veins are not so common. The costa never has any accessory branches. The subcosta normally has none, but there is occasionally a tendency for their development (e.g. Lesina blanchardi).

R_1 sometimes has accessory branches near the tip of the wing (e.g. Acridoxena hewaniana, Lesina blanchardi, and many Phaneropterines). MA occasionally has accessory branches in addition to its two main branches (which may be regarded as primary). MP (or $MP+Cu_{1a}$) almost invariably gives rise to an anterior accessory branch: this feature is constant enough

to warrant the use of a separate name - MP_a. As mentioned above MP_a is occasionally replaced by an intercalary vein, IMA.

No definite accessory veins are found in the cubito-anal lobe, apart from Cu_{1a} and Cu_{1b}; these (and their counterparts in the fore wing) are regarded as pseudo-primary veins (see p. 28) and are dealt with accordingly.

(iii) The cross-veins.

In the evolution of most insect wings the formation of cross-veins is accompanied by the reduction and disappearance of the primitive archedictyon. Although this is largely true of the Tettigoniid hind wing, in the fore wing the formation of cross-veins has not resulted in the loss of the archedictyon: both are typically found together in the spaces between the longitudinal veins. This is no doubt correlated with leaf-mimicry, as the resulting pattern resembles closely the arrangement of veinlets typical of many deciduous leaves.

The most strongly developed cross-veins in the fore wing are generally found in the subcostal, radial, first radial, and anterior medial, areas. They are also frequently developed in areas C, R_s, and MA.

In the hind wing the membrane between the longitudinal veins is generally supported entirely by cross-veins, but there is a tendency in some forms for these to be replaced by archedictyon towards the distal extremity of the wing (see below).

(iv) The archedictyon.

In the Tettigoniidae the archedictyon generally extends over the whole of the fore wing (except for parts of the stridulatory apparatus in the male). Representative types of Tettigoniid archedictyon are shown in Fig. 56.

The hind wing usually has no archedictyon, but in some forms a small area of it is found towards the distal part of the wing. This is characteristic of the subfamily Phaneropterinae, in which this part of the hind wing normally protrudes from under the fore wing when the wings are at rest. Archedictyon is also found in the hind wings of Salomona pupus, Macroxiphus, Acridoxena hewaniana, Hexacentrus, and Sathrophyllia.

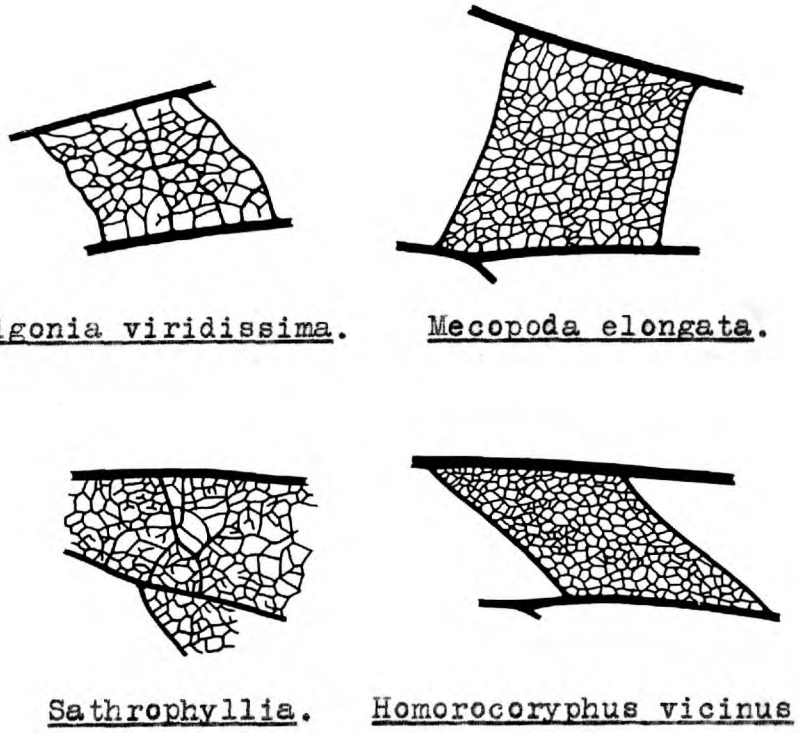


Fig.56. Types of Tettigoniid fore wing archedictyon.

XVII. TETTIGONIOIDEA - SCHIZODACTYLIDAE

1. INTRODUCTION

No work has previously been published on the homologies of the wing-veins of Schizodactylus, the only winged genus in this family. The description below refers to the fully-winged species of this genus.

No nymphs were available, but the tracheation could be seen in the adult wings.

2. THE SHAPE AND AREAS OF THE WINGS

(a) Fore wing.

When flexed the wings of Schizodactylus are folded in such a way that their more distal regions form a spike which is rolled upwards into a tight spiral over the apex of the abdomen. Because of this unique feature the venation of both pairs of wings (see Fig. 57) is very much modified. As in the Gryllidae the fore wings form a box-like cover for the hind wings, their more basal regions being folded longitudinally for this purpose along the centre (in the region of the radius). More distally this fold runs into the enormous medio-cubital fan, the base of which acts in the same way as the median fan of the Gryllidae, allowing the fore wings to close in over the tapering abdomen.

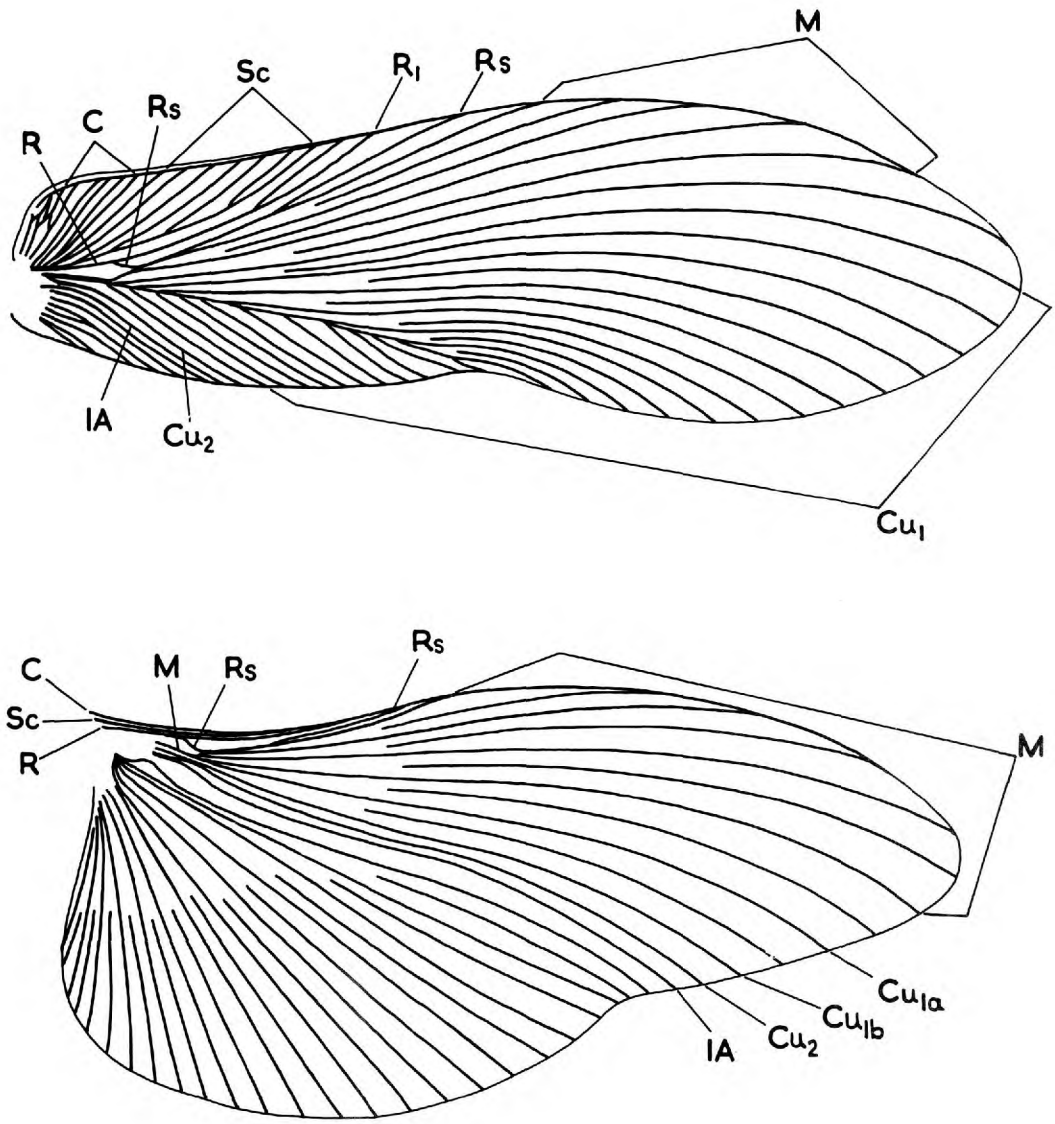


Fig.57. The wings of Schizodactylus.

As in the Gryllidae the areas of the fore wing cannot be labelled satisfactorily using the Comstock-Needham System. An alternative scheme is shown in Fig. 58; further subdivisions are probably unnecessary.

The texture of the lateral and dorsal fields of the fore wings of Schizodactylus is rather tough (very similar to that of many large Gryllid fore wings); the medio-cubital fan, on the other hand, is thin and membranous.

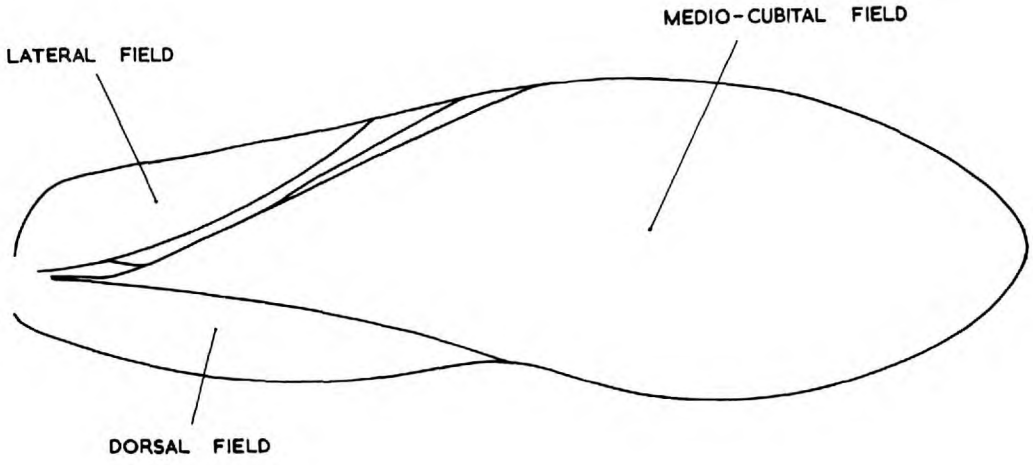
(b) Hind wing.

The hind wings of Schizodactylus only differ from the usual Orthopterous shape in having the pre-anal part greatly enlarged, so as to be about equal in area to the anal lobe. The more distal region of the pre-anal area forms a spirally-rolled spike when the wing is flexed.

The areas of the hind wing are shown in Fig. 58, labelled on the basis of the Comstock-Needham System. The costal and subcostal areas are very reduced; area M is greatly enlarged.

3. FOLDING.

It is the unique nature of the medio-cubital fan ~~of the fore wing~~ and the way in which it is folded which has led to the extreme modification of the venation of Schizodactylid fore wings. The base of the fore wing folds into two halves in the Gryllid fashion, but in the position occupied by the median fan in the Gryllidae an enormous outgrowth has taken place, resulting in the development of the extensive distal lobe, supported by the



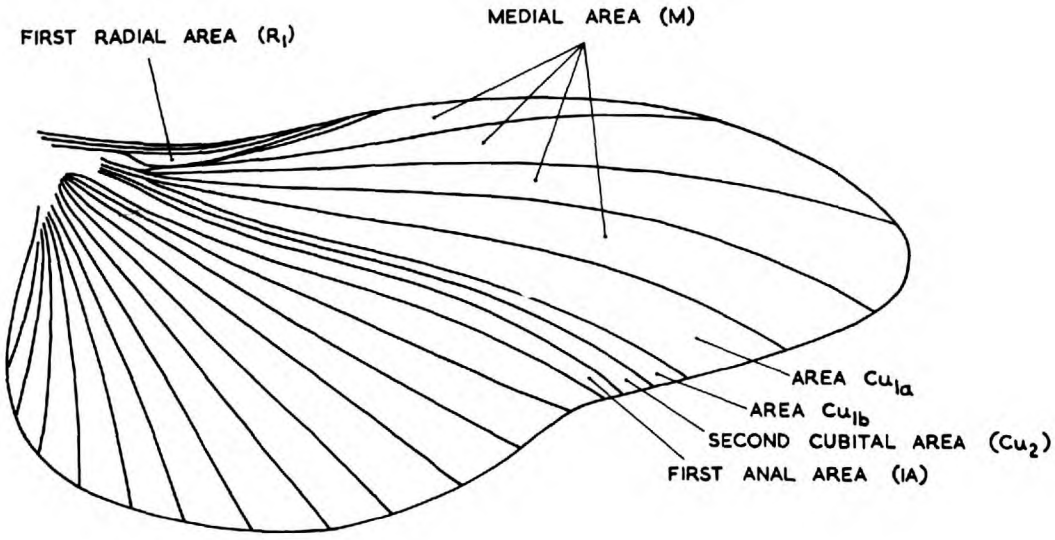


Fig.58. The areas of Schizodactylid wings.

media and anterior accessory branches of Cu_1. This medio-cubital fan is pleated longitudinally, there being concave folds between the primary and intercalary veins, which are both convex. The basal part of the fan functions in the same way as the Gryllid median fan; the more distal part folds into a long spike, from which is formed the characteristic roll at the back of the folded wings.

The hind wings fold in a manner similar to those of the Gryllidae; the resulting spike, however, is rolled upwards as in the fore wing.

4. THE VEINS

The veins of Schizodactylid wings may be classified in the same way as those of the Pneumoridae, and the various types are defined under ~~this~~ that family (see p. 66 et seq.).

(a) The ambient veins.

In the fore wings of Schizodactylus an ambient vein is developed proximally, just behind the anterior margin. More distally the anterior margin becomes supported by primary veins. There is also an ambient vein close to the posterior margin of the dorsal field. These two veins may be referred to as the anterior ambient vein (AA) and posterior ambient vein (PA), respectively. The posterior margin of the medio-cubital fan is unsupported.

There are no ambient veins in the hind wing.

(b) The longitudinal veins.

(i) Primary veins.

THE COSTA (C)

The more proximal of the supporting veins in the lateral field of the fore wing receive tracheae from a stem separate from that giving rise to the tracheae supplying the remaining veins in this field. It is probable that these two groups correspond to the costa and subcosta, respectively, and they are regarded as such here.

In the hind wing a rather feeble costa is developed along the anterior margin; its function is taken over distally by the subcosta, radius, and media, in turn.

The costa is slightly convex in the hind wing, but shows no tendencies in this respect in the fore wing.

THE SUBCOSTA (Sc)

In the fore wing this vein lies well back from the anterior margin and gives rise to a number of anterior accessory branches, supporting the more distal part of the lateral field.

In the hind wing the subcosta runs just behind the costa in the most basal part of the wing, but soon replaces it on the wing margin.

The subcosta tends to be slightly concave in the fore wing and is more definitely so in the hind wing.

THE RADIUS (R)

In the fore wing the radius runs parallel to and a short distance behind the subcosta. It divides near the base of the wing into two branches, R_1 and R_s. R_1 runs directly to the

wing-margin; R_s immediately fuses to the most anterior of the medial branches for part of its length, separating again before reaching the wing-margin. The free base of R_s has the appearance of an oblique cross-vein.

The radius is very similar in the hind wing, but here R_1 runs much closer to Sc and is unbranched.

R and R_1 tend to be convex in the fore wing and are markedly so in the hind wing.

THE MEDIA (M)

In both pairs of wings the main stem of the media is very short; it divides near the wing-base into three or four parallel branches. These support the anterior part of the medio-cubital field in the fore wing and an equivalent area in the hind wing.

The branches of the media are convex, lying along the convex ridges of the medio-cubital fan.

THE CUBITUS (Cu)

As in other Orthoptera this vein divides at its base into two branches, Cu_1 and Cu_2. In the fore wing Cu_1 is highly modified due to the development of the medio-cubital fan; it gives rise to a number of accessory branches on both sides, supporting the posterior part of the medio-cubital field and the more distal part of the dorsal field.

In the hind wing Cu_1 is divided near the base of the wing into two equally developed branches, Cu_{1a} and Cu_{1b}.

Cu_2 is unbranched in both pairs of wings. In the hind

wing it is very feebly developed, becoming obsolete towards the wing-margin.

The anterior accessory branches of Cu_1 in the fore wing lie along the convex ridges of the medio-cubital fan. In the hind wing Cu_{1a} and Cu_{1b} are also convex, occupying similar positions. Cu_2 shows no definite tendencies in this respect in either wing.

THE ANALS

In the fore wing there ~~are~~ is a number of parallel anal veins, of which the most anterior probably corresponds to 1A in other Orthoptera. They support the more proximal part of the dorsal field.

The anal veins of the hind wing are of the usual Orthopterous type. The most anterior one (1A) is the most strongly developed and runs parallel to Cu_2. The remaining anals are arranged radially and support the anal fan. The exact determination of their homologies is impossible (see pp. 45 and 28).

(ii) Secondary veins.

A. Intercalary veins.

There are numerous intercalary veins in the wings of Schizodactylus, always associated with the folding of the medio-cubital or anal fans.

In the fore wing there are intercalary veins between the branches of M, and between the anterior branches of Cu_1. This is also true of the hind wing; here there are also

intercalary veins between the anals.

These intercalary veins are all convex, and, together with the primary veins with which they alternate, form the convex ribs of the medio-cubital and anal fans. The concave folds between these ribs are not supported by veins.

B. Accessory veins.

These veins are numerous in Schizodactylid fore wings. The costa and subcosta give rise to several accessory branches supporting the lateral field. R_1 has one accessory branch in Schizodactylus, and Cu_1 bears a large number of both anterior and posterior accessory branches supporting parts of the medio-cubital and dorsal fields. The veins behind 1A in the fore wing must be partly of an accessory nature as they are more numerous than was primitively the case.

There are no accessory veins in the hind wing other than of the pseudo-primary type (see p. 28).

XVIII. TETTIGONIOIDEA - CONCLUSIONS

The Tettigonioidea are a very diverse group, and there is no diagnostic character of the wing-venation common to all the winged families. The most characteristic feature is the fusion between Cu_1 and MP, especially in the fore wing. This is found in the Prophalangopsidae, Tettigoniidae, and some Gryllacrididae. The Schizodactylidae are quite independent from the remaining Tettigonioidea, and there are characters in their wings which suggest that they are more related to Grylloid stock than to the Tettigonioidea. The following characters of Schizodactylid wings are found elsewhere among the Orthoptera only in the Grylloidea:-

1. The characteristic folding of the fore wing along the more basal regions of R, M, and Cu.

2. The development of the median fan in the fore wing.

3. The extension of the fan-like folding to the most anterior branch of M in both pairs of wings.

4. The spike formed by the distal end of the flexed hind wing (coiled in Schizodactylus).

5. The basal division of Cu_1 into two branches (which remain separate) in the hind wing.

These characters tend to suggest that the Schizo-

dactylidae originated from early Grylloid stock, before the fourth tarsal segment was lost. There does not, however, appear to be any other morphological support for this.

As discussed in Section VI, the early Prophalangopsidae were probably ancestral to both the remaining Tettigonioidea and the Grylloidea. The numerous anterior accessory branches of Sc in the fore wings of this family are also found in the Grylloidea, Schizodactylidae, and, to a rather less extent, Tettigoniidae.

The fossil family Elcanidae also has a distinctive wing-venation, though here the differences are mainly of degree only. The most interesting feature of the fore wing is its primitive corrugation; the unaltered convexities and concavities are much more extensive than in any other Tettigonioid family (see p. 50 et seq.). Other distinctive features of the Elcanid fore wing are the enormous radial sector (occupying about half the wing-area) and the well-developed posterior media, which is quite free from Cu_1. There is little doubt, even on the evidence supplied by the fore wings alone, that the Elcanid line was quite distinct from that of the remaining Tettigonioidea and quite possibly even of their immediate Protorthopteran ancestors. The free posterior media and primitive corrugation are of great significance, making it almost certain that the Elcanidae have been quite independent from the Prophalangopsidae.

Gryllacridid wings do not present any features of

outstanding importance. The veins of the fore wing are characteristically arranged in parallel longitudinal lines, this probably being associated with the wrapping function of the wing when flexed. There is often an unusually large number of anal veins. In the hind wings the fusion between R, M, and Cu_1 has advanced to a unique extent.

The wings of the Prophalangopsidae are of great interest in providing a link between Protorthopteran stock and the Tettigoniidae, and in showing the gradual evolution of the stridulating organ. In the fore wing the accessory branches of the subcosta are characteristically numerous, and the closely parallel arrangement of the cross-veins in the fossil forms is unique. The hind wing is a rather more primitive version of the Tettigoniid hind wing, lacking the fusion between R_s and M (which, however, is not an invariable feature in the Tettigoniidae - see p. 129). Prophalangopsis has a rather more advanced fore wing than the fossil forms, especially in the structure of the stridulating organ and the arrangement of the cubital branches.

The Tettigoniid venation is of the Prophalangopsid type with the following additional specializations:-

1. The development of the mirror in the stridulatory apparatus.

2. The complete distal fusion of MP with the most anterior branch of the cubitus.

3. The fusion between R_s and MA in the hind wing.

4. The development of the cubital hinge in the fore wing.

There is little doubt, however, that the two families are closely related, the following characters being common to both and not normally found in other Tettigonioidea:-

1. The alary stridulatory organ.

2. The partial fusion of MP with the most anterior branch of the cubitus.

3. The development of Cu_{1a} in the hind wing.

XIX. GRYLLOIDEA - GRYLLIDAE

1. INTRODUCTION

Previous work on the homologies of the wing-veins of the Gryllidae is scanty. Comstock and Needham (1899, and Comstock, 1918) described and illustrated the tracheation of Oecanthus, but did not correlate this with the adult venation. Forbes (1933) published diagrams of the female adult wings of Nemobius fasciatus (De Geer) and Oecanthus, partly basing his conclusions on the nymphal tracheation of Scapteriscus didactylus (Latreille), a member of the Gryllotalpidae. In 1939, Zeuner gave an account of the venation of the fossil Gryllidae and of Brachytrypes (of which he also gives a figure of the nymphal tracheation); his conclusions were based mainly on fossil wings. Chopard (1940) applied a nomenclature similar to that of the Comstock-Needham System to Gryllid fore wings and attempted to correlate the male venation with that of the female. Unfortunately, this author made no use of the nymphal tracheation, which, as a result, conflicts with his views. Later (in Grassé, 1949) Chopard published an interpretation of Gryllid venation differing fundamentally from his earlier conclusions.

The correspondence between the nomenclatures of various authors is shown in Fig. 59.

NOMENCLATURE IN THIS WORK	SYMBOL	COMSTOCK (1918)	FORBES (1933)	ZEUNER (1939)	CHOPARD (1949)	BRUNNER (1882)	SAUSSURE (1870)
Subcosta	Sc	Subcosta	Subcosta	Subcosta	Subcosta	Radial	Mediastinal
Radius	R	Radius	Radius	Radius	Radius	Anterior ulnar	Humeral
Media	M	Media	Media	Media	Media	Posterior ulnar	Median
Cubitus-one	Cu_1	Cubitus-one	Third plical?	Cubitus	Cubitus	Vena dividens	Discoidal
Cubitus-two	Cu_2	Cubitus-two			Anal	Vena plicata	Second discoidal
First anal	1A	First anal			Axillaries		Anal
Second anal	2A						Axillaries
Third anal	3A						

(a) Female fore wing

NOMENCLATURE IN THIS WORK	SYMBOL	COMSTOCK (1918)	ZEUNER (1933)	CHOPARD (1949)	BRUNNER (1882)	SAUSSURE (1870)
Subcosta	Sc	Subcosta	Subcosta	Subcosta	Radial	Mediastinal
Radius	R	Radial	Radial	Radial	Anterior ulnar	Humeral
Media	M	Media	Media	Media	Posterior ulnar	Median
Cubitus-one	Cu_1	Cubitus-one	Cubitus	Cubitus	Vena dividens	Discoidal
Cubitus-two	Cu_2	Cubitus-two	First anal	Anal	Vena plicata	Second discoidal
First anal	1A	First anal	Second anal	Axillaries		Anal
Second anal	2A		Third anal			Axillaries
Third anal	3A		Fourth anal			

(b) Male fore wing

Fig. 59. Comparative table showing the nomenclatures used by various authors for Gryllid wing-veins.

NOMENCLATURE IN THIS WORK	SYMBOL	COMSTOCK (1918)	FORBES (1933)	BRUNNER (1882)	SAUSSURE (1870)
Costa	C				Mediastinal
Subcosta	Sc	Subcosta	Subcosta	Anterior radial	
Radius	R	Radius	Radius	Middle radial	
Radius-one	R_1		Radius-one		
Radial sector	R_s		Radial sector		
Media	M	Media	Media	Posterior radial	
Anterior media	MA		M_{1+2}		Humeral
Posterior media	MP		M_{3+4}		Median
Branches of	Cu_{1a}	Cubitus-one	Cubitus-one	Anterior ulnar	Discoidal
Cubitus-one	Cu_{1b}		Cubitus-two	Posterior ulnar	
Cubitus-two	Cu_2	Cubitus-two	First plical	Vena dividens	
First anal	1A	First anal	Second plical	Vena plicata	Anal

(c) Hind wing

Fig. 59. Comparative table showing the nomenclatures used by various authors for Gryllid wing-veins (contd.).

2. THE TRACHEATION OF THE NYMPHAL WING-PADS

(a) Fore wing-pad.

A short costal trachea with several accessory branches is present in Acheta and Brachytrypes, but is probably not a usual feature outside the Gryllinae.

The subcostal trachea is well-developed and usually bears a number of anterior accessory branches. There is an unbranched radial trachea.

The medial, cubital, and anal tracheae are closely associated at their bases. Trachea M is often bifurcate. The cubital trachea is normally divided into Cu_1 and Cu_2; its nature is usually very different in the two sexes. In the female fore wing-pad Cu_1 has typically several posterior accessory branches towards its distal extremity; the Cu_2 trachea has several accessory branches in the Gryllinae and usually two in the other subfamilies. The Cu_1 trachea of the male fore wing-pad supplies the mirror, the anterior and distal borders of the harp, and in many Gryllines and Oecanthines it has in addition a number of posterior accessory branches at its extremity. The Cu_2 trachea supplies the posterior border of the harp, and is usually unbranched. There are usually three anal tracheae.

(b) Hind wing-pad.

A small costal trachea is sometimes present (e.g. Acheta domestica Linnaeus, Fig. 60). The subcostal trachea is unbranched. Trachea R is usually divided into R_1 and R_s, but may be unbranched. As in the fore wing-pad, the medial,

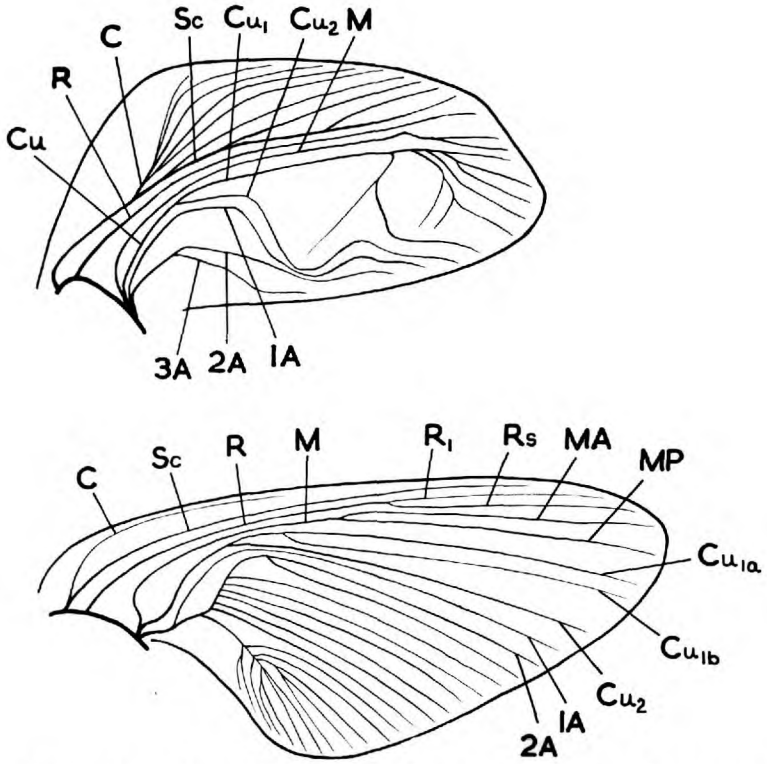


Fig.60. The tracheation of the nymphal wing-pads of Acheta domestica, male.

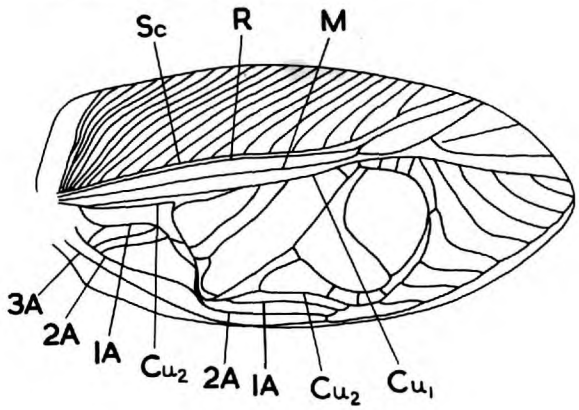


Fig.63. The male fore wing of Eneoptera.

cubital, and anal tracheae arise at the same point on the transverse basal trachea. M is typically divided into MA and MP. Cu is invariably three-branched, the branches being Cu_{1a}, Cu_{1b}, and Cu_2. As is usual in Orthopteroid insects, the first anal trachea has an origin distinct from that of the remaining anal tracheae, which are often numerous.

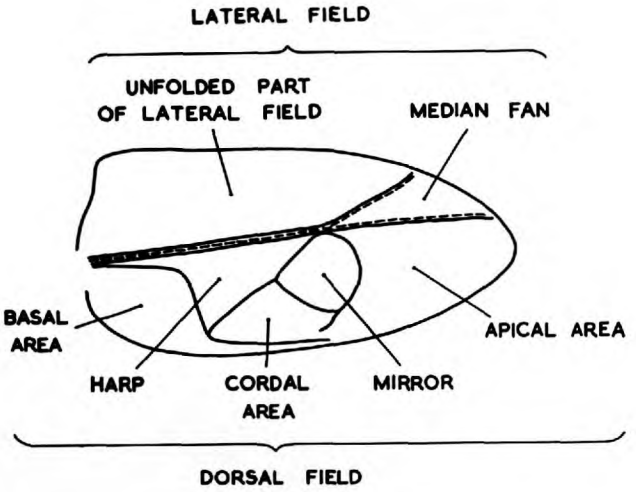
3. THE VENATION OF THE ADULT WINGS

(a) The shape and areas of the wings.

(i) Fore wing.

When at rest Gryllid fore wings typically form a box-like cover for part of the hind wings and all but the ventral part of the abdomen. For this purpose they fold longitudinally near the centre, where there are a number of closely parallel main veins. Allowance is normally made for the tapering shape of the abdomen by means of another (fan-like) fold in the distal part of the wing; this occurs along the branches of the media, and may be called the median fan (see Fig. 61). The consistency of the fore wing is usually tough and leathery, and in some forms the membrane is fairly heavily sclerotized (e.g. Trigonidium).

The shape of the fore wing varies considerably, but is not typically more than three times longer than it is broad, unlike the normal condition in most other Orthoptera. In the males of Phaeophilacris the fore wings are lobe-shaped with a constricted base. Brachypterous and apterous forms are common in the family.



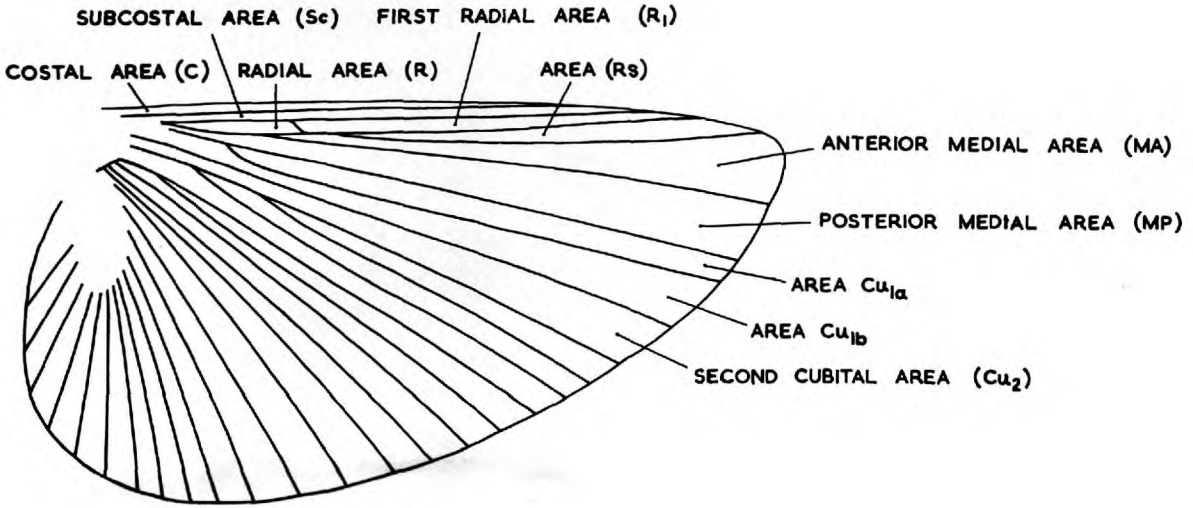


Fig.61. The areas of Gryllid wings.

It is impossible in the male and difficult in the female to name the areas of the fore wing satisfactorily using the Comstock-Needham System. An alternative system for the male (partly based on systems used in the past) is shown in Fig. 61. Owing to the way in which the flexed fore wing is folded, it may be clearly divided into dorsal and lateral fields. It is the dorsal field of the male fore wing which has become modified for stridulation in most forms. This region may be divided in the male into five subdivisions:-

1. the basal area
2. the harp
3. the mirror
4. the cordal area
5. the apical area

Of these the first four are modified for stridulation, the last being unaffected. The apical area is sometimes practically absent (e.g. Oecanthus) and is usually very reduced in brachypterous forms (e.g. the brachypterous species of Gryllodes). The harp is typically about twice the area of the mirror, but in Paragryllus temulentus Saussure the two areas are approximately equal, and in Homeogryllus the mirror is slightly larger than the harp.

The female fore wing generally has a well-developed median fan, but the dorsal field is never modified for stridulation.

(ii) Hind wing.

Gryllid hind wings are typically Orthopterous, being

in the form of a foldable fan with the main veins arranged radially. The length of the hind wings is typically greater than that of the fore wings: sometimes twice their length (e.g. Nemobius fasciatus; Euscyrtus), or even up to four times longer (e.g. some species of Paranemobius).

The areas of Gryllid hind wings are easily named using the Comstock-Needham System; a proposed scheme is given in Fig. 61.

(b) Folding.

The folding of the fore wing, as mentioned above, is typically such that it forms a box-like cover for the proximal part of the flexed hind wings and the dorsal and lateral parts of the abdomen. Additional folding occurs at the distal end of the lateral field, forming the median fan; this fan is normally shorter (in comparison with the wing-length) in the male than in the female. The arrangement of these folds is shown in Fig. 61.

The hind wings fold up in a similar way to those of the Tettigonioidea, but the folding is rather more complete, extending up to the anterior margin of the wing. The folds are usually supported by veins.

(c) The wing-base.

In the axillary region of each wing is a number of sclerites connecting the bases of the wing-veins to the thoracic tergum. The wing-base of Acheta domestica (see Fig. 62) may

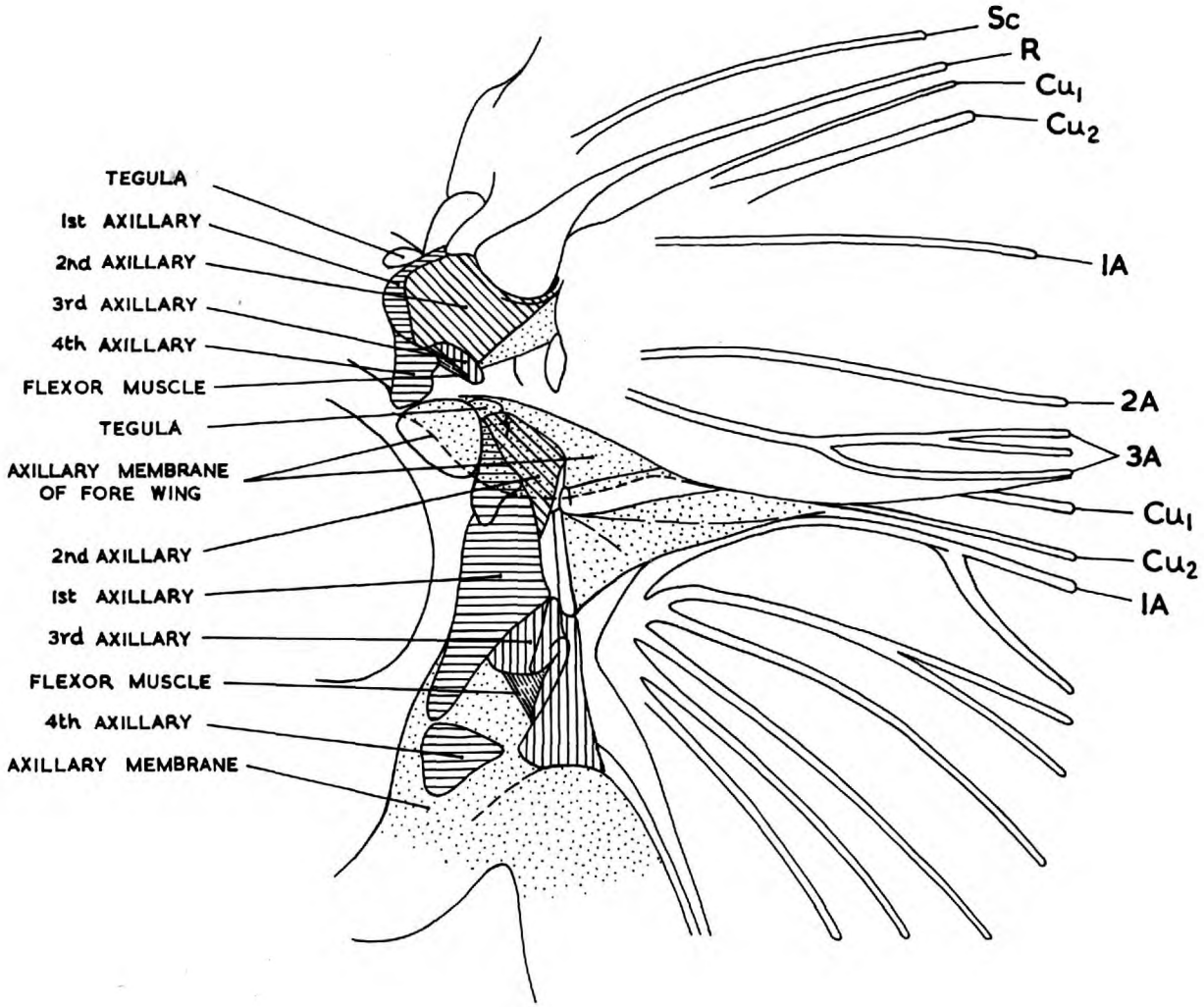


Fig.62. The wing-bases of Acheta domestica.

be regarded as typical of the family; the base of each wing is described separately below.

(i) Fore wing.

The first axillary sclerite, situated between the mesonotum and second axillary, articulates with the base of the subcosta. Just anterior to it is a small tegula. The second axillary is very large and provides an articulation for the base of the radius. Protruding from under this sclerite is a small third axillary, inserted on which is the flexor muscle of the fore wing.

As in the Tettigoniidae there is a well-developed fourth axillary, connecting the posterior part of the wing-base to the mesonotum.

There are no median plates.

(ii) Hind wing.

In the hind wing the first axillary is a very large sclerite, articulating with a large part of the metanotum. The costa is fused at the base with the subcosta, radius, and media, and has lost its connection with the first axillary. As in the fore wing there is a tegula at the anterior extremity of this sclerite.

The second axillary is normally developed and provides an articulation for the fused bases of C, Sc, R, and M.

The anal veins are supported at the base by the third axillary, which bears the flexor muscle of the hind wing. Between this sclerite and the posterior extremity of the first

axillary is a small but well-developed fourth axillary.

The median plates may be represented by small thickenings of the axillary membrane.

(d) The veins.

The veins of Gryllid wings may be classified in the same way as those of the Pneumoridae, and the various types are defined under ~~this~~ that family (see p. 66 et seq.).

(i) The ambient veins.

No constant ambient veins occur in the Gryllidae, though a tendency towards their formation is shown by the fore wings of many members of the family. There are never any ambient veins in the hind wing.

In the fore wing feebly developed ambient veins are sometimes found near the margins of the lateral field and towards the apex of the dorsal field. In the former position the ambient vein is usually formed by the tips of the numerous accessory veins arising from the costa (when present) and subcosta, and in the latter position by the accessory branches of Cu_1 and Cu_2 (Cu_1 only in the male). Ambient veins of this type are developed to some extent in the male fore wings of Eneoptera (see Fig. 63). In males of the genus Oecanthus (see Fig. 64) extensions of 1A and 2A round the cordal area and harp have taken up an ambient position. Ambient veins are developed in the reduced fore wings of Trigonidium (Fig. 65).

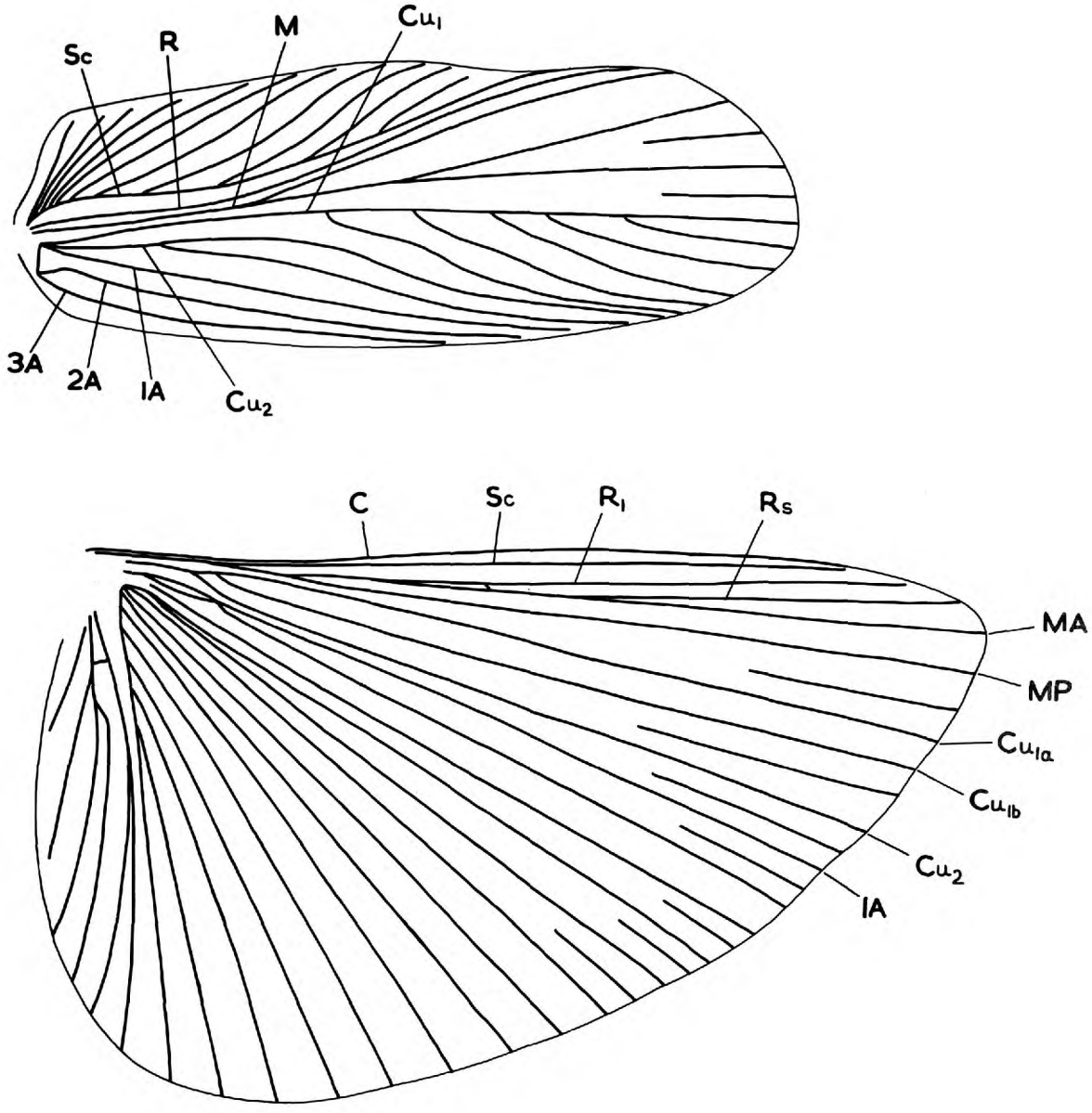
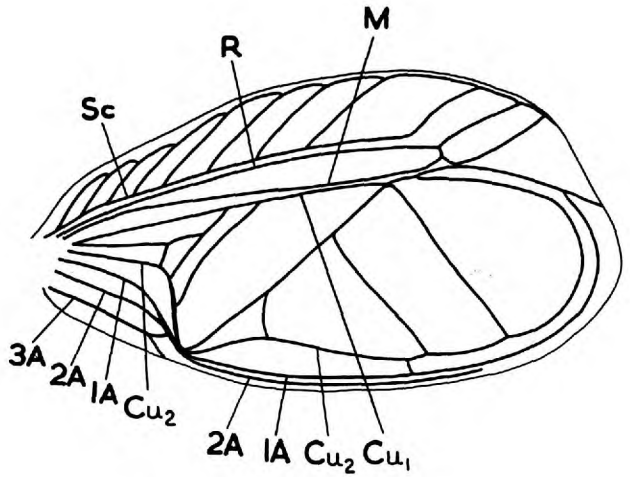
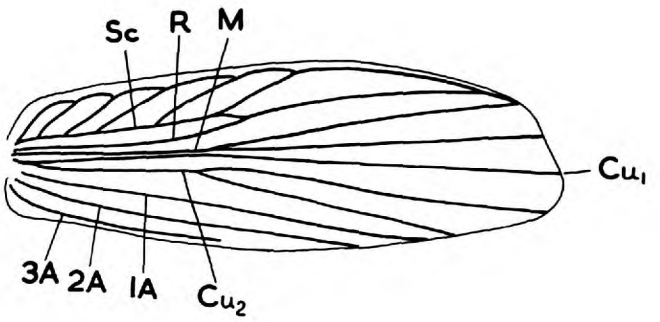


Fig.63. The wings of Eneoptera, female.



Male fore wing.



Female.

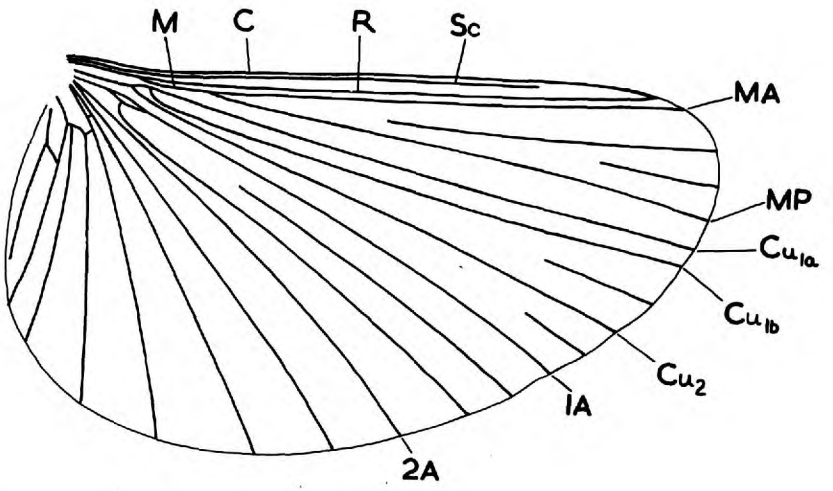
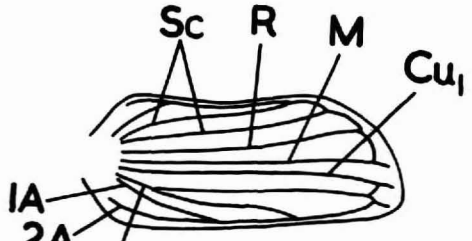
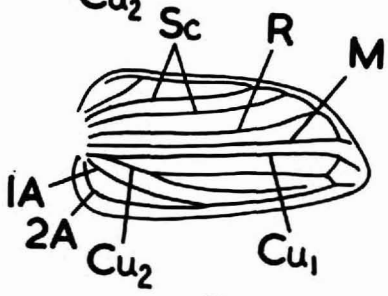


Fig.64. The wings of Oecanthus pellucens.



Male fore wing.



Female.

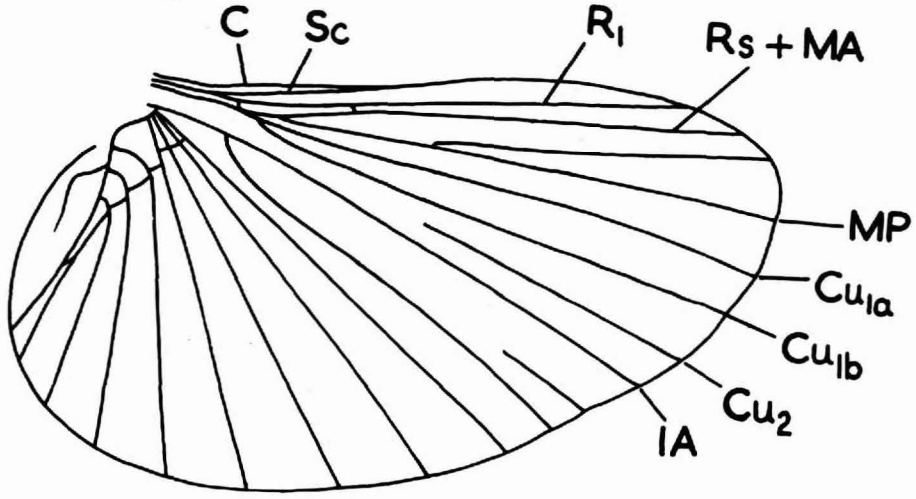


Fig.65. The wings of
Trigonidium humbertianum.

(ii) The longitudinal veins.

A. Primary veins.

THE COSTA (C)

In the fore wings of most Gryllids the costa is either absent or incorporated in the subcosta. Sometimes, however, the first apparent branch of the subcosta is much more strongly developed than the remainder, and is probably the costa. This condition is found in Acheta domestica (see Fig. 66).

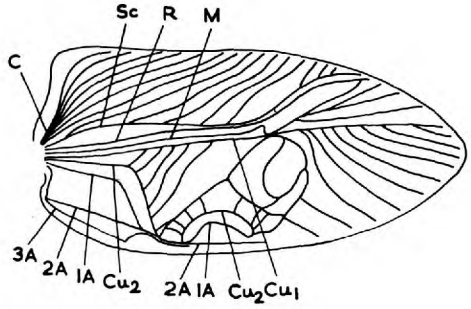
The costa forms the whole or, more usually, the proximal part of the leading edge of the hind wing. Towards the distal part of the wing it is sometimes replaced or reinforced by the subcosta (e.g. Eneoptera, Trigonidium). When the costa extends over the whole of the anterior margin of the hind wing (e.g. Oecanthus pellucens (Scopoli)) it is convex. More usually, however, its tendencies in this respect are very feeble.

THE SUBCOSTA (Sc)

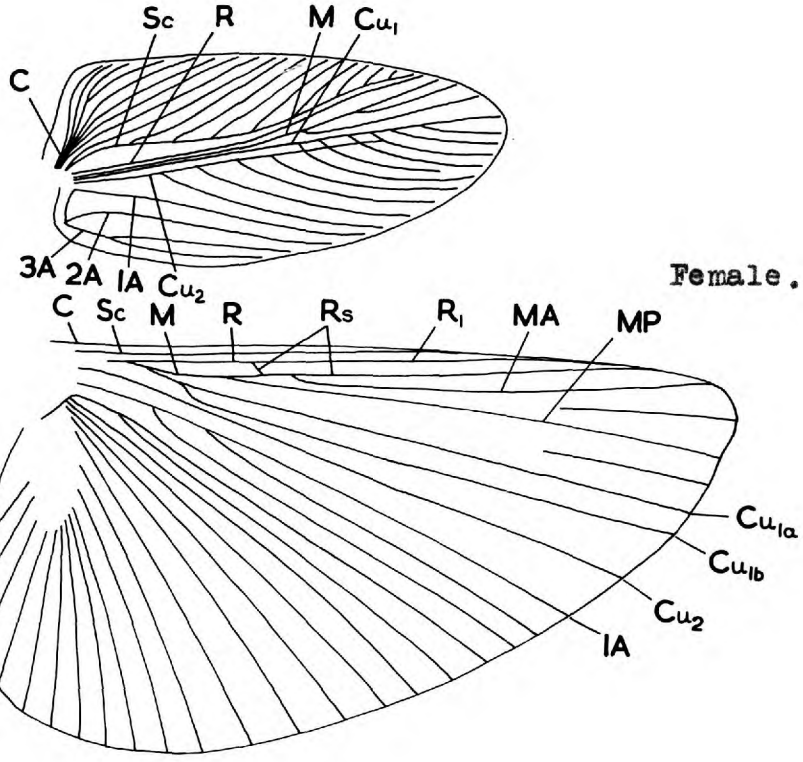
The subcosta is the first normally developed primary vein in the fore wing. It lies well behind the anterior margin, the area between the two being supported by its accessory branches, which are often numerous.

In the hind wing this vein runs just behind the costa, frequently fusing with or replacing it distally.

The subcosta shows no definite convexity or concavity in the fore wing. When the costa is well-developed in the hind wing (e.g. Oecanthus pellucens) the subcosta is concave;



Male fore wing.



Female.

Fig.66. The wings of Acheta domestica.

usually, however, this concavity is lost and a tendency towards convexity is shown, especially in the distal part of the wing.

THE RADIUS (R)

In the fore wing this vein runs just behind the subcosta and is always unbranched. An unbranched radial sector (R_s) is, however, normally present in the hind wing, where it is typically fused to MA for a variable distance. The division of the radius into R_1 and R_s is normally about halfway to the apex or in the proximal half.

The radius tends to be convex in both pairs of wings.

THE MEDIA (M)

The media lies just behind the radius in the fore wing. It typically gives rise to a variable number of branches which support the folds of the median fan.

In the hind wing the media normally divides into two equally developed branches in the proximal half. The anterior branch is generally fused with R_s for a greater or lesser part of its length, and frequently the media or its anterior branch is fused to the main stem of the radius.

The nature of the media and its branches (i.e. whether it is an anterior, posterior, or complete media in the Lameerian sense (Lameere, 1922)) is discussed on pp. 58 and 59.

THE CUBITUS (Cu)

The cubitus is divided at or very near the base into two branches, Cu_1 and Cu_2. In the fore wing these branches normally show marked sexual dimorphism, being much modified for

stridulation in the male. In this sex Cu_1 runs parallel to M to a region near the base of the median fan, where it divides forming a number of accessory branches. The more distal of these support the apical area, when present, and the remainder delimit the mirror and form the boundary between the cordal area and harp. Cu_2 runs roughly parallel to Cu_1 for a short distance and then abruptly bends towards the hind wing-margin. Near the latter it fuses with 1A and 2A, this region being known as the node. These veins then separate to form the three cords which are characteristic of male Gryllid fore wings. In the Gryllinae Cu_2 and 1A commonly form an enclosed loop in the cordal area. The stridulatory teeth occur on the part of Cu_2 anterior to the node, on the underside of both fore wings. They vary in number considerably throughout the family: there are about 40 to 50 in Oecanthus and Eneoptera, and about 150 in Acheta domestica.

The female fore wing shows no specialization for stridulation. Cu_1 passes straight down the longitudinal axis of the wing, typically giving rise to posterior accessory branches towards the apex. In Oecanthus pellucens Cu_1 may be unbranched in the female fore wing. Cu_2 runs close behind Cu_1; it is often bifurcate (e.g. Eneoptera; Trigonidium humbertianum (Saussure)), but tends to give rise to a number of posterior accessory branches in the Gryllinae.

In the hind wing Cu_1 is divided at its base into two parallel, equally developed branches (Cu_{1a} and Cu_{1b}); these run straight to the wing-margin. The more distal part of the

area between them (area Cu_{1a}) is pigmented in many species. Cu_2 shows a tendency towards reduction in Gryllid hind wings. It is always feebly developed towards the base, and only the distal part remains in Trigonidium humbertianum.

THE ANALS

As these are completely different in the two pairs of wings, they will be dealt with separately.

Fore wing.

There are normally three anal veins in Gryllid fore wings (1A, 2A, and 3A). As with the cubitus they show sexual dimorphism. In the male 1A and 2A fuse with Cu_2 at the node and then separate again forming the second and third cords. 3A runs closely behind 2A, reaching the posterior wing-margin just before the node. In the female the three veins run parallel to the wing margin; 2A and 3A may be fused at the base.

In the fore wings of Trigonidium humbertianum there are only two anal veins.

Hind wing.

The first anal (1A) is a very strongly developed vein in the hind wing. It runs parallel to and just behind Cu_2 to the wing-margin. Sometimes this vein has posterior accessory branches (e.g. Acheta domestica).

The second and remaining anal veins can be given no definite homologies (see pp. 45 and 28). They are more numerous than in the Tettigonioidea and Acridoidea, and vary considerably in number: there are about seven in Oecanthus and about twenty

in the larger species of Gryllus Linnaeus.

B. Secondary veins.

Intercalary veins.

There are frequently no intercalary veins in Gryllid fore wings; in some of the larger forms, however, there are a few intercalary veins developed in the median fan (e.g. Eneoptera).

Intercalary veins are nearly always developed in the hind wings, though usually confined to areas MA, MP, Cu_{1b}, Cu_2, and 1A.

Accessory veins.

These veins are usually profusely developed in Gryllid fore wings. The subcosta almost invariably gives rise to a number of anterior accessory branches supporting the lateral field. In the female Cu_1 frequently bears several posterior accessory branches towards the distal part of the wing. This is almost invariably so in the male fore wing, where these branches support the apical area, the mirror, the distal margin of the harp, and the anterior margin of the cordal area.

Cu_2 is often bifurcate in the female fore wing, forming two equally developed pseudo-primary veins (see p. 28); sometimes, however, it gives rise to a number of posterior accessory branches (e.g. many Gryllinae). In the male fore wing Cu_2 is very rarely ~~never~~ branched.

The anal veins are frequently unbranched in the fore wing, but sometimes one of them bears one or two accessory

branches (e.g. 3A in Acheta domestica, female).

In the hind wing there are no accessory veins in the pre-cubital part of the wing. Cu_1 is divided into two pseudo-primary veins (see p. 28). Some of the veins supporting the anal fan (particularly 1A) may give rise to non-tracheated accessory veins.

(iii) The cross-veins.

These veins are abundantly developed in Gryllid hind wings and female fore wings, but in a number of male fore wings there are remarkably few. In the fore wings of male Acheta domestica, for example, the cross-veins in the lateral field, anal area, and cordal area, are very few and poorly developed; the only strongly developed cross-veins are the three or four forming the 'strings' of the harp, one in the mirror, and a number in the apical area. There are even fewer in the male fore wings of Oecanthus, the apical area being absent. Cross-veins also tend to be poorly developed in the female fore wings of some small species.

(iv) The archedictyon.

There is never much archedictyon in Gryllid wings: it is normally found only as a trace near the wing-bases. Occasionally, however, a small amount of archedictyon persists in the distal part of the dorsal field (e.g. Eneoptera). In some forms there is no archedictyon (e.g. Oecanthus pellucens; Trigonidium humbertianum).

XX. GRYLLOIDEA - GRYLLOTALPIDAE

1. INTRODUCTION

Practically no work has been published in the past on the homologies of Gryllotalpid wing-veins. Comstock and Needham made no mention of the family. Forbes (1933) published diagrams of the wings and wing pads of Scapteriscus, but his text gives them no more than a passing reference; this work is the only published instance of wing-tracheation studies in the family. Zeuner (1939) has discussed the wing-venation of the Gryllotalpidae, but his conclusions were based on Gryllid and fossil wings rather than on tracheation.

A comparison between the views of these authors, together with Martynov's nomenclature for the hind wing of Gryllotalpa gryllotalpa (Linnaeus) (Martynov, 1925), is given in Fig. 67.

2. THE TRACHEATION OF THE NYMPHAL WING-PADS

Where the tracheation of Scapteriscus is mentioned, the conclusions are drawn from the diagrams of Forbes (1933), which are reproduced in Fig. 68.

(a) Fore wing-pad.

In Scapteriscus there is a short trachea arising from the base of trachea Sc which is probably homologous with the

NOMENCLATURE IN THIS WORK	SYMBOL	FORBES (1933)	ZEUNER (1939)	BRUNNER (1882)	SAUSSURE (1870)
Subcosta	Sc	Subcosta	Subcosta	Radial	Mediastinal
Radius	R	R and R+M	Radius	Ulnar	Humeral
Media	M	M and Cu_1, Cu_2, 1Pl	Media	Vena dividens	Median
Cubitus-one	Cu_1	1Pl, Ax	Cubitus		Discoidal, Anal
Cubitus-two	Cu_2		First anal		Axillaries
First anal	1A		Second anal		
Second anal	2A		Third anal		
Third anal	3A		Fourth anal		

(a) Fore wing

NOMENCLATURE IN THIS WORK	SYMBOL	MARTYNOV (1925)	FORBES (1933)
Subcosta	Sc	Subcosta	Subcosta
Radius	R		Radius
Radius-one	R_1	Radius	Radius-one
Radial sector	R_s	Media	Radial sector
Anterior media	MA		M_{1+2}
Posterior media	MP		M_{3+4}
Branches of Cubitus-one	Cu_{1a}	Cu	Cubitus-one
	Cu_{1b}	Cusp	Cubitus-two
Cubitus-two	Cu_2	A_1	First plical
First anal	1A	A_2	Second plical

(b) Hind wing

Fig. 67. Comparative table showing the nomenclatures used by various authors for Gryllotalpid wing-veins.

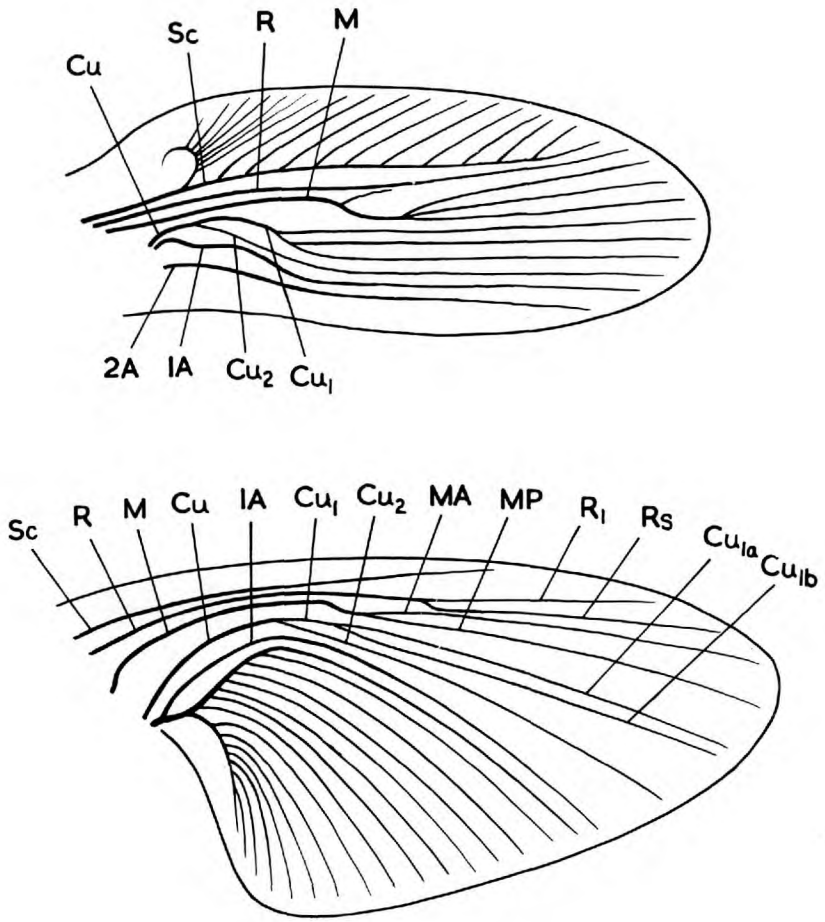


Fig.68. The tracheation of the nymphal wing-pads of Scapteriscus didactylus (Latreille), female. After Forbes (1933).

costal trachea of the Gryllidae (when present). It bears several accessory branches. Gryllotalpa (see Fig. 69) has no costal trachea in the fore wing-pad.

The subcostal trachea resembles that of typical Gryllidae; arising from it are a number of anterior accessory branches. The radial trachea is either unbranched or bifurcate distally.

In Scapteriscus the medial trachea is sharply bent about halfway along its length; here it gives rise to a feebly developed anterior branch, which runs obliquely towards the radial trachea. The remainder of the medial trachea then divides into two or three parallel branches which extend to the margin of the wing-pad; this applies to the female only - in the male the remainder of trachea M is probably unbranched. In Gryllotalpa the medial trachea is either unbranched or bifurcate at the tip.

As in all typical Orthoptera, the cubital trachea gives rise to an undivided posterior branch (Cu_2) near its base. Trachea Cu_1 is always branched.

There are usually three anal tracheae.

(b) Hind wing-pad.

There was no costal trachea in the nymphs examined.

The subcostal trachea is normally developed and unbranched. Trachea R is divided into R_1 and an unbranched radial sector (R_s). The medial trachea is simply bifurcate into MA and MP.

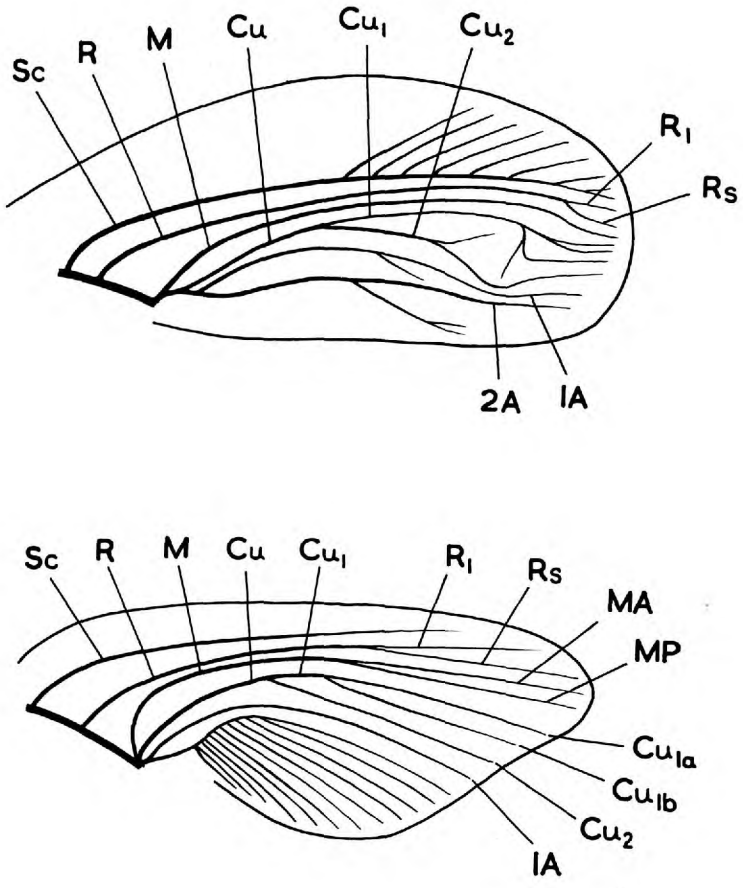


Fig.69. The tracheation of the nymphal wing-pads of Gryllotalpa gryllotalpa, male.

As in all Grylloidea the cubital trachea is divided into a bifurcate anterior branch (Cu_1) and an undivided posterior branch (Cu_2); the resulting three tracheae run parallel to the margin of the wing-pad.

The first anal trachea has an independent base from the remaining anal tracheae, which are numerous. None of the anal tracheae is branched.

3. THE VENATION OF THE ADULT WINGS.

(a) The shape and areas of the wings.

(i) Fore wing.

Gryllotalpid fore wings are lobe-like and generally cover only the basal part of the abdomen and hind wings. In some species of Scapteriscus, however, the fore wings almost reach the tip of the abdomen. The texture of the fore wing is fairly soft, but not so membranous and transparent as that of the hind wing.

As in the Gryllidae the fore wing may be divided into dorsal and lateral fields, the media forming the dividing line. The Gryllid median fan is not found in the Gryllotalpidae. A harp of the Gryllid type is developed in the dorsal field of the male fore wing, but other subdivisions are better named using the Comstock-Needham System (see Fig. 70).

(ii) Hind wing.

As in other Orthoptera the hind wings take the form of a fan, folded when at rest. They are longer than the

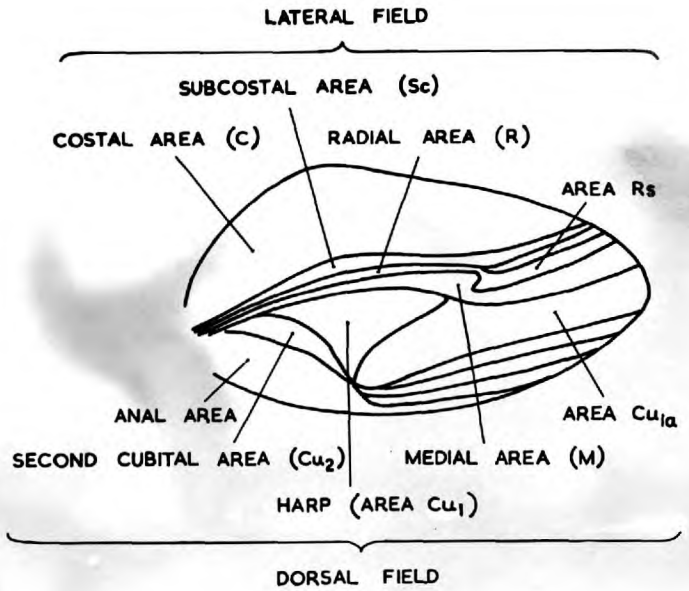
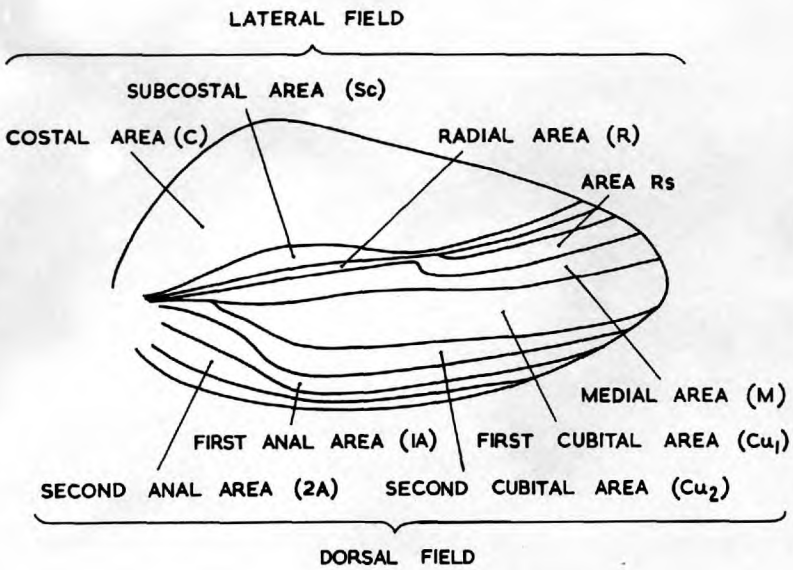
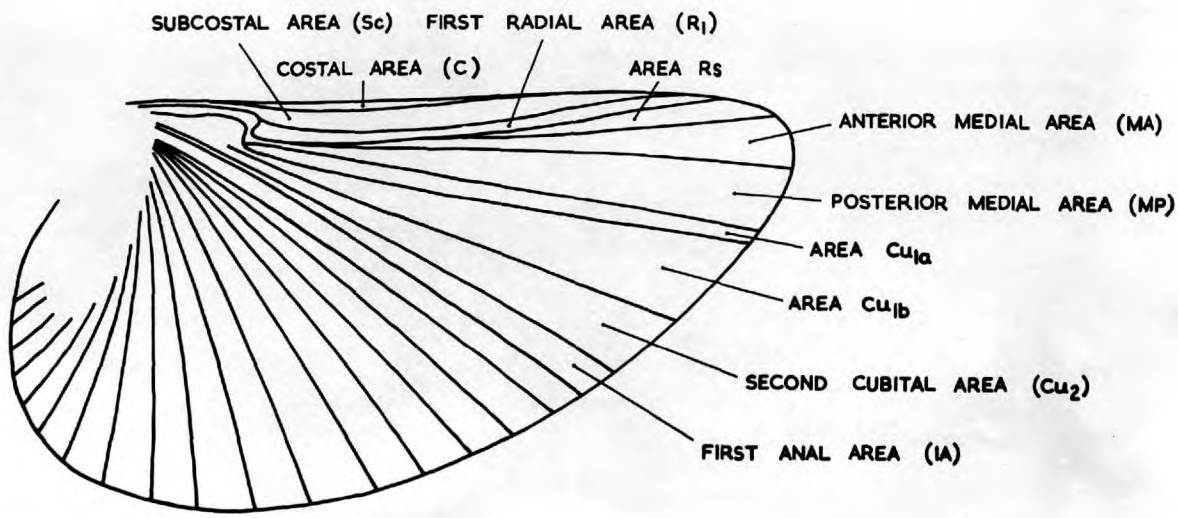


Fig.70. The areas of Gryllotalpid wings.

Male fore wing.



Female.



fore wings and often extend beyond the tip of the abdomen.

A proposed scheme for naming the areas of Gryllotalpid hind wings, using the Comstock-Needham System, is shown in Fig. 70.

(b) Folding.

The flexed fore wings are folded rather obtusely along the region of the media. Although there is no median fan, additional folding does tend to take place at the distal wing-margin, especially between R_s and M.

The hind wings are folded in the Gryllid fashion, areas Sc and Cu_{1a} being dorsally exposed and therefore pigmented.

(c) The veins.

The veins of Gryllotalpid wings may be classified in the same way as those of the Pneumoridae, and the various types are defined under ~~this~~ that family (see p. 66 et seq.).

(i) The ambient veins.

No definite ambient veins are developed in Gryllotalpid wings. There is, however, sometimes a tendency for the tips of some of the accessory subcostal branches to bend over along the anterior margin of the wing and join with each other, thus forming a short marginal support which could be looked upon as an ambient vein.

(ii) The longitudinal veins.

A. Primary veins.

THE COSTA (C)

No normally developed costa is found in Gryllotalpid fore wings. In Scapteriscus, however, the first reflexed branch arising from the subcostal stem is probably homologous with the Gryllid costa.

In the hind wing a reduced costa is developed along the more proximal part of the anterior margin. The remainder of the leading edge of the wing is supported by the subcosta.

THE SUBCOSTA (Sc)

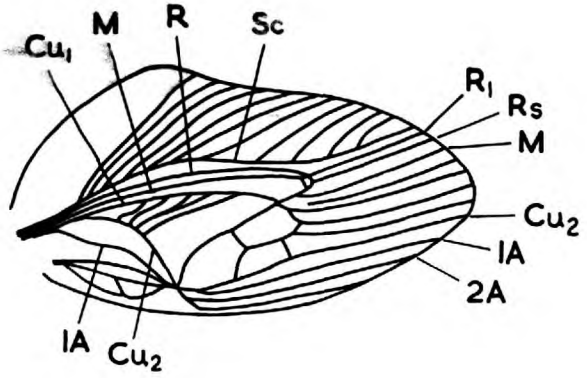
This is the first fully developed primary vein in the fore wing. As in the Gryllidae it lies well behind the anterior margin and gives rise to a row of accessory branches supporting the anterior part of the wing.

In the hind wing the subcosta runs close behind the costa in the proximal part of the wing and replaces it on the anterior margin distally. Normally more than half of the leading edge of the hind wing is supported by the subcosta.

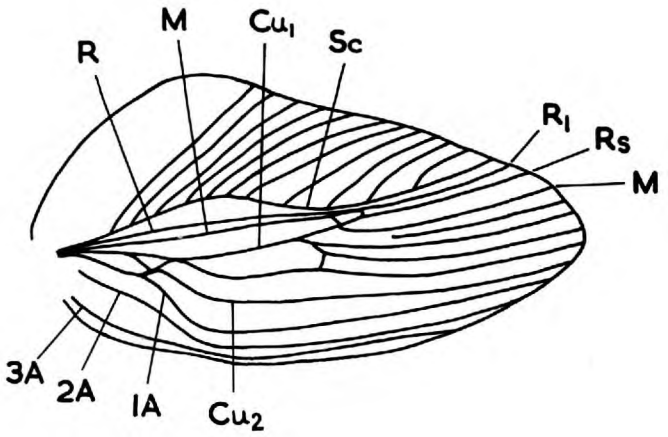
The subcosta is rather concave in the hind wing, but shows no definite tendency in this respect in the fore wing.

THE RADIUS (R)

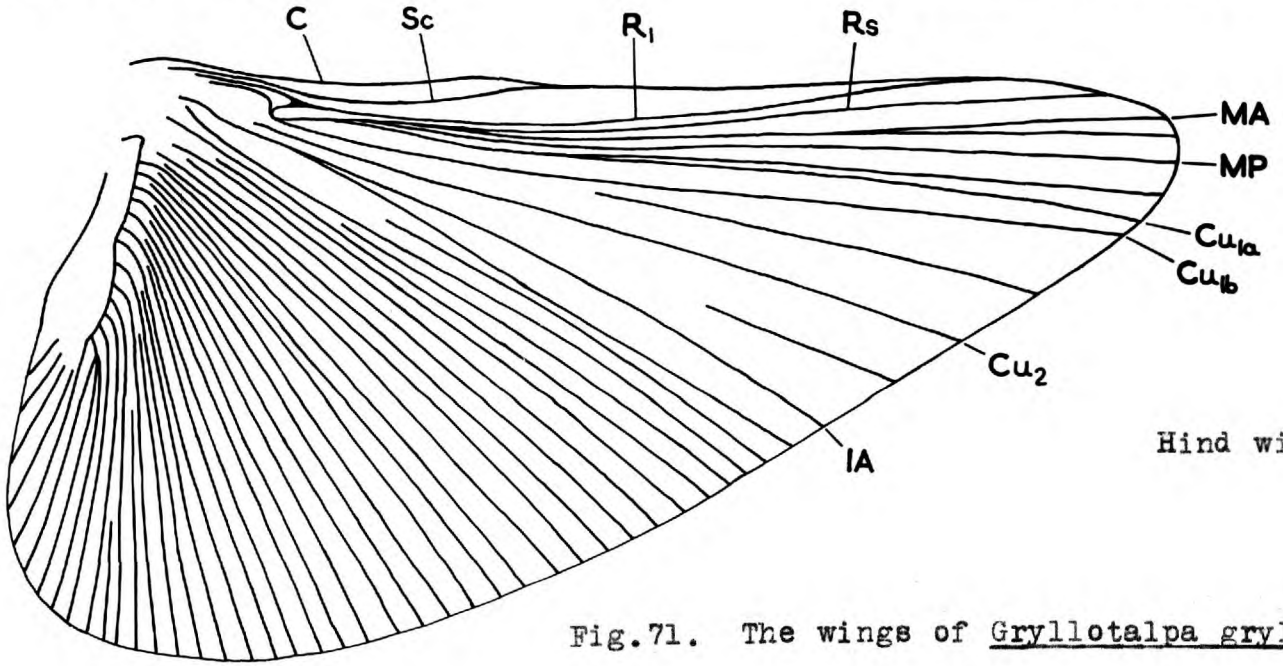
This vein runs parallel to and a short distance behind the subcosta. In the fore wings of Gryllotalpa (see Fig. 71) it becomes divided distally into two branches, R_1 and R_s, which run parallel with each other to the wing-margin. In



Male fore wing.



Female fore wing.



Hind wing.

Fig.71. The wings of Gryllotalpa gryllotalpa.

Scapteriscus, however, R_s is reduced in the male and absent in the female (see Fig, 72).

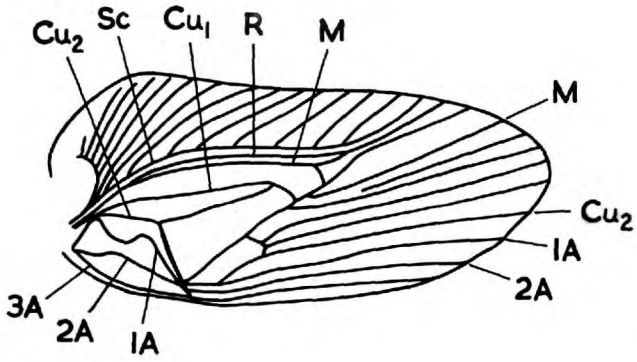
In the hind wing the bifurcation of the radius takes place near the wing-base. R_s becomes fused to MA for a short distance, as in the Gryllidae.

The radius shows no convexity or concavity in the fore wing, but in the hind wing R and R_1 are convex and R_s tends to be concave.

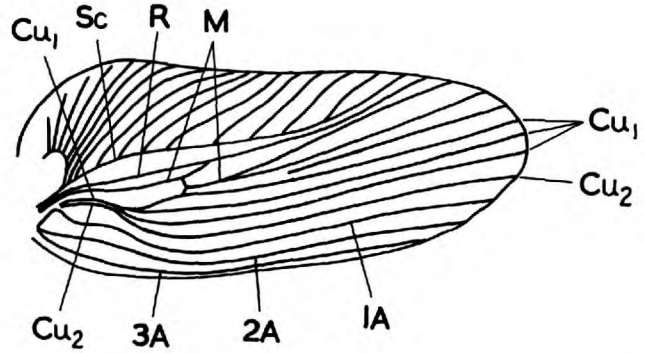
THE MEDIA (M)

This vein lies just behind the radius. In the fore wing the media is sharply bent at one place along its length. At the point where this bend occurs (usually in the distal half of the wing, but nearer the base in females of Scapteriscus) an anterior branch leaves the media and joins the radius. This branch has the appearance of a longitudinal vein but is actually a cross-vein. At the second part of the bend (where the media resumes its longitudinal course) another cross-vein connects it to Cu_1. After this double bend the media runs straight to the wing-margin. It is unbranched in the fore wings of Gryllotalpa and male Scapteriscus, but in the females of Scapteriscus the media becomes divided into two or three branches.

In the hind wing the media is of the Gryllid type, being divided near the base of the wing into two equally developed branches (MA and MP). It shows no definite convexities or concavities in either pair of wings.



Male fore wing.



Female.

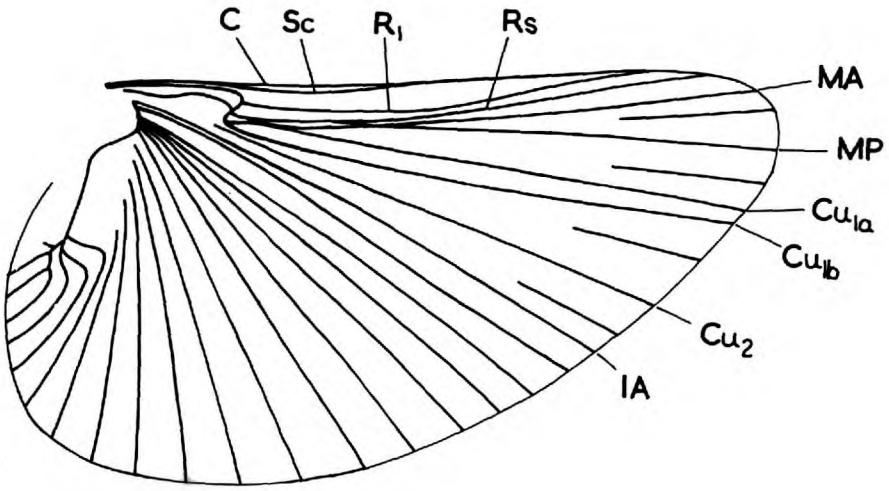


Fig.72. The wings of Scapteriscus.

The branches of the media in the Gryllotalpidae undoubtedly have the same status as those of the Gryllidae; the remarks on pp. 58 and 59 concerning the nature of the Gryllid medial branches (sensu Lameere, 1922) also apply, therefore, to the Gryllotalpidae.

THE CUBITUS (Cu)

As in other Orthoptera the cubitus divides at or near the wing-base into Cu_1 and Cu_2. In the fore wing these branches show a similar sexual dimorphism to that found in the Gryllidae. In both sexes Cu_1 runs parallel to M and a short distance behind it, becoming divided into two or three branches; these branches arise nearer to the base in the female than in the male. The most proximal branch in the male is reflexed, and forms the distal boundary of the harp, as in the Gryllidae; the remaining branches support the apical region of the wing.

Cu_2 is unbranched and runs parallel to the last branch of Cu_1 in the female fore wing, but in the male this vein becomes bent towards the posterior wing-margin forming the proximal boundary of the harp and bearing the stridulatory teeth; it then continues towards the apex of the wing.

In the hind wing the cubitus is of the Gryllid type: Cu_1 is divided near its base into two equally developed branches, Cu_{1a} and Cu_{1b}, and Cu_2 is unbranched, running straight to the wing-margin. Area Cu_{1a} is pigmented or darkened distally, as in some Gryllidae.

The cubitus shows no definite convexities or concavities.

THE ANALS

There are normally three anal veins in Gryllotalpid fore wings. In the male, at least 1A and 2A fuse with Cu_2 at a point corresponding to the Gryllid node; they then separate and run parallel to each other to the wing-margin. In the female no fusion takes place, though in some species Cu_2 and 1A are closely approximated at the wing-base.

To the anal veins of the hind wing the same remarks apply as those ~~given for~~ made about the Gryllidae (see p. 160).

B. Secondary veins.

Intercalary veins.

The only intercalary vein in the Gryllotalpid fore wing is situated between M (or its most posterior branch) and Cu_1. It is probable that it originated as an accessory branch, as there are often signs of a reduced base connecting it to M or Cu_1.

In the hind wing intercalary veins are quite common. In Scapteriscus there is an intercalary vein in each of the areas MA and MP; these are replaced by accessory veins in Gryllotalpa. There are always intercalary veins in areas Cu_{1b} and Cu_2. In Gryllotalpa there are intercalary veins between the anal veins, but in Scapteriscus they are very feebly developed or absent.

Accessory veins.

In the fore wing the subcosta bears a number of anterior accessory veins in the same way as in the Gryllidae. Cu_1 becomes divided into two or three pseudo-primary branches

(see p. 28) in the female; in the male this vein gives rise to several accessory branches which form the boundaries of some of the resonant areas used in stridulation. The apical region of the male fore wing is also partially supported by branches of Cu_1.

Some of the oblique veins running across the harp are supplied with tracheae arising from Cu_2; these could, therefore, be regarded as accessory veins.

(iii) The cross-veins.

There are numerous cross-veins in both fore and hind wings.

(iv) The archedictyon.

In Gryllotalpid wings the archedictyon is only found as a trace at or near the bases of both pairs of wings.

XXI. GRYLLOIDEA - CONCLUSIONS

This superfamily is clearly defined and shows no great diversity of form. The following features of the wings are characteristic:-

1. The development of the harp and associated structures in the stridulatory organ.

2. The numerous, closely parallel, sinuous, anterior accessory branches of the subcosta in the fore wing.

3. The reduction or complete absence of the costa.

4. The division of Cu_1 into two free branches in the hind wing, and the frequent sclerotization or loss of transparency between them (developed because of the characteristic method of folding).

5. The method of folding the hind wings so as to form a spike, generally protruding beyond the fore wings.

6. The close approximation of Sc, R, M, and Cu_1, along the mid-longitudinal line of the fore wing.

It should be noted that features 2, 3, and 5, are not quite diagnostic in the Saltatoria as they are also found in the Schizodactylidae (see p. 146).

The Gryllotalpidae represent an offshoot from the Gryllid line, specialized for burrowing and a subterranean mode of life. They do not possess the mirror and cords of Gryllid wings, and the median fan is only very slightly developed.

XXII. DICTYOPTERA - INTRODUCTION & BLATTOIDEA

1. INTRODUCTION

Although much work has been done on cockroach wings, Mantoid wing-venation has been almost completely ignored in the past. Comstock and Needham (1899, and Comstock, 1918) described and illustrated the adult venation of Phyllodromia germanica (Linnaeus) and the wing-pad tracheation of some unnamed cockroach nymphs. Handlirsch (1908) has published labelled drawings of the wings of various Blattoid and Mantoid species. Martynov has given illustrations of the hind wing of Blatta orientalis Linnaeus (Martynov, 1937) and the fore wing-base of a Mantoid species (Martynov, 1925). Forbes (1933) illustrates wings of various cockroaches and a mantis, and proposes modifications to the Comstock-Needham terminology. Chopard (in Grasse, 1949) gives diagrams of Blattoid and Mantoid venation. Rehn (1951) gives a comprehensive comparative account of cockroach venation, mainly using Forbes' nomenclature. The most recent work on Dictyopteran venation is that of Smart (1951), who describes and illustrates the venation and tracheation of Periplaneta americana (Linnaeus).

Tracheation has been extensively used in studying

Blattoid wing-venation, but there has apparently been no previous work on Mantoid tracheation. The present account is a mere summary in the case of the Blattoidea, and no more than an introduction to the tracheation and venation of the Mantoidea.

The rest of this Section is devoted to the former superfamily, while the Mantoidea are dealt with in Section XXIII.

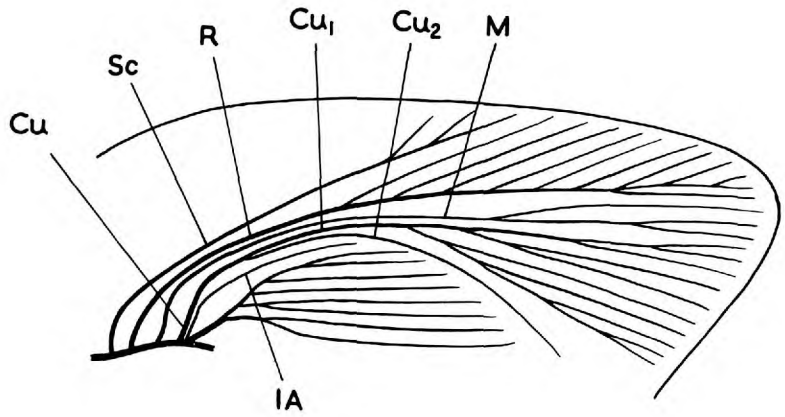
2. SYNONYMY

A comparison between the vein terminology of various authors is given by Smart (1951). The nomenclatures of Forbes, Rehn, and the pre-Comstock systematists are, however, omitted from this comparison; these are tabulated by Rehn (1951) (Rehn's nomenclature differs from that of Forbes only in being more detailed). The nomenclature in the present work (which corresponds exactly with Comstock and Needham's views on cockroach venation) differs from that of Smart (op. cit.) only in that the postcubitus and vannal veins (names proposed by Snodgrass, 1935) are all regarded as anal veins (see p. 73).

3. THE TRACHEATION OF THE NYMPHAL WING-PADS

This has been dealt with by Comstock and Needham (1899, and Comstock, 1918), Beck (1920), and Smart (1951).

The transverse basal trachea is apparently not always present. The costal trachea is poorly developed or absent. Otherwise, the tracheation is quite normal, corresponding closely with the adult venation. A diagram showing the typical form of Blattoid wing-pad tracheation is given in Fig. 73.



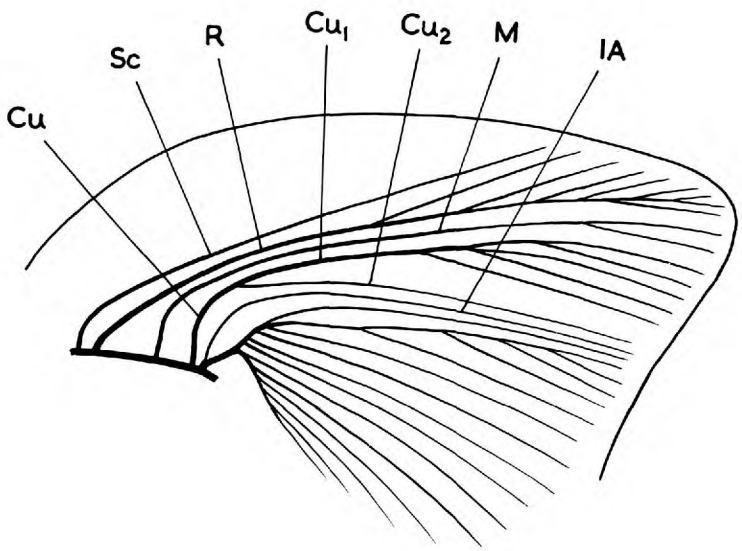


Fig.73. The typical form of Blattoid wing-tracheation.

4. THE VENATION OF THE ADULT WINGS

A diagram representing the venation of typical Blattoid wings is given in Fig. 74.

The costa lies along the leading edge of both pairs of wings, but is very reduced and possibly absent in some forms. The subcosta is generally well-developed and may bear anterior accessory branches. A strongly developed radius is always present; in the fore wing this vein gives rise to a characteristic row of accessory branches supporting a large area (area Sc) in the anterior part of the wing. A posterior branch, which possibly represents R_s, is developed in the more primitive fore wings, but is often reduced or absent in the more specialized groups. In the hind wing the radius has a similar form; the radial sector may be represented either by the small posterior branch, which is only developed in the more primitive wings, or by all but the most proximal of the anterior branches, which tends to have an appearance rather distinct from the remainder.

The media is normally developed and dichotomously branched in primitive Blattoids, but becomes reduced to a single stem in the more advanced forms.

The cubitus divides at its base into Cu_1 and Cu_2. Cu_1 is normally much branched, covering a large area, but in some hind wings it is reduced to a single stem. Cu_2 (the 'first plical' of Forbes) is normally unbranched; in the fore wing it is poorly developed, forming the hind margin of the cubital furrow ('plical furrow' of Rehn; 'posterior unsclerotized line'

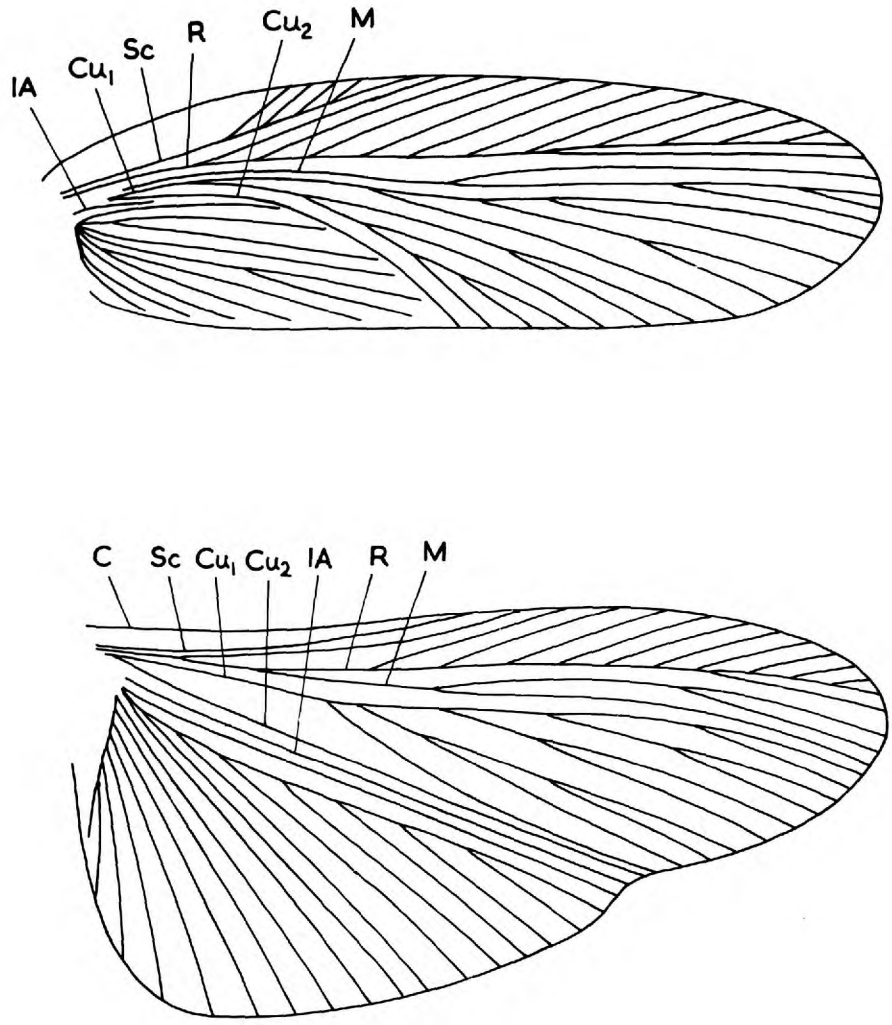


Fig.74. The typical venation of Blattoid wings.

of Smart).

The first anal vein is often invisible ~~not normally visible~~ in the fore wing, being situated in the heavily sclerotized anterior part of the anal area, just behind Cu_2. In the hind wing 1A (the 'second plical' of Forbes) is well-developed in the more primitive forms, but in the more advanced groups it often becomes very reduced, especially towards the wing-margin.

In the fore wing there are several anal veins in the anal area; these may be looked upon as 2A, 3A, etc., but their exact homology is impossible to determine. The second anal vein of the hind wing (the 'third plical' of Forbes) is quite distinct from the remainder, a feature very characteristic of Blattoid wings. As in the fore wing no definite homologies can be ascribed to the veins of the anal area (see pp. 45 and 28).

XXIII. DICTYOPTERA - MANTOIDEA

1. SYNONYMY

No work on the tracheation of Mantoid nymphal wing-pads and no detailed work on the adult venation has apparently been done in the past, but various authors have expressed views on the latter and these are tabulated in Fig. 75.

2. THE TRACHEATION OF THE NYMPHAL WING-PADS

The tracheation of the wing-pads of Ameles heldreichi Brunner (Fig. 76) and Sphodromantis viridis (Forskal) (Fig. 77) were examined and the following remarks apply to these two species.

There is no costal trachea. The subcostal trachea is well-developed and normal. The radial trachea is normal and divides distally into R_1 and R_s. This bifurcation is much nearer the base in the hind wing-pad than in the fore wing-pad. The medial trachea is either unbranched or bifurcate distally.

The cubital trachea becomes divided near the base into Cu_1 and Cu_2. Trachea Cu_1 is branched, especially in the fore wing; trachea Cu_2 is undivided. The first anal trachea has an independent origin from the remaining anals, which arise from a

NOMENCLATURE IN THIS WORK	SYMBOL	HANDLIRSCH (1925)	MARTYNOV (1925)	CHOPARD (1949)	BRUNNER (1882)	SAUSSURE (1871)
Costa	C	Costa		Costa		
Subcosta	Sc	Subcosta		Subcosta	Mediastinal	Mediastinal
Radius	R	Radius			Anterior radial	Humeral
Radius-one	R_1			R		
Radial sector	R_s			R_s		
Media	M	Media			Posterior radial	Median
Cubitus-one	Cu_1		Cu	Cu Cup	Anterior ulnar	Discoidal
Cubitus-two	Cu_2		A_1	Anal	Posterior ulnar	Anal
First anal	1A		A_2		Vena dividens	Axillaries
Second anal, etc.	2A, etc.		A_3	Axillaries	Vena plicate	

(a) Fore wing

NOMENCLATURE IN THIS WORK	SYMBOL	CHOPARD (1949)	BRUNNER (1882)	SAUSSURE (1871)
Costa	C	Costa		
Subcosta	Sc	Subcosta	Mediastinal	
Radius	R			Humeral
Radius-one	R_1	R	Anterior radial	
Radial sector	R_s	R_s	Middle radial	
Media	M	Media	Posterior radial	Median
Cubitus-one	Cu_1	Cu	Anterior ulnar	Discoidal
Cubitus-two	Cu_2	Cup	Posterior ulnar	Anal
First anal	1A	Anal	Vena dividens	
Second anal, etc.	2A, etc.	Axillaries		Axillaries

(b) Hind wing

Fig. 75. Comparative table showing the nomenclatures used by various authors for Mantoid wing-veins.

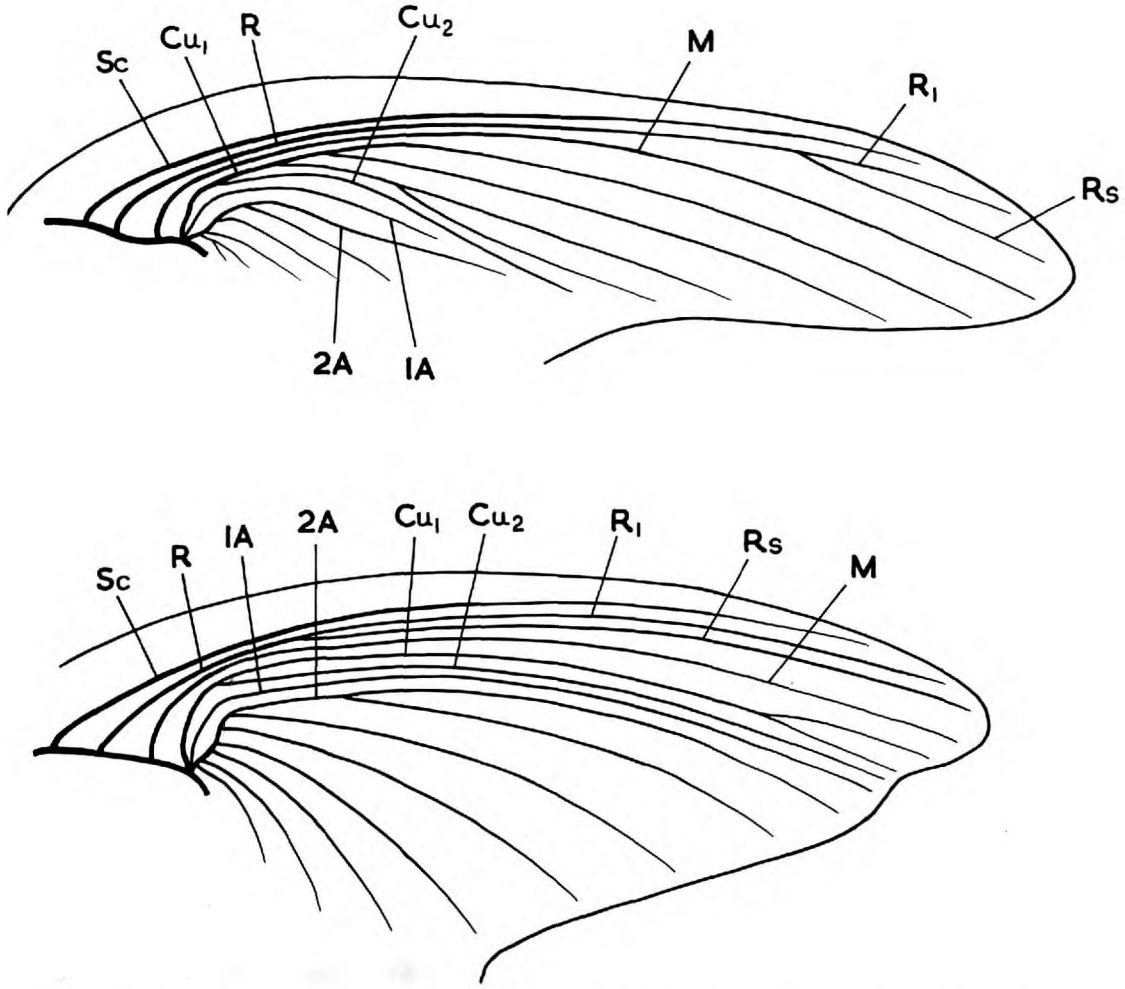


Fig.76. The tracheation of the nymphal wing-pads of Ameles heldreichi.

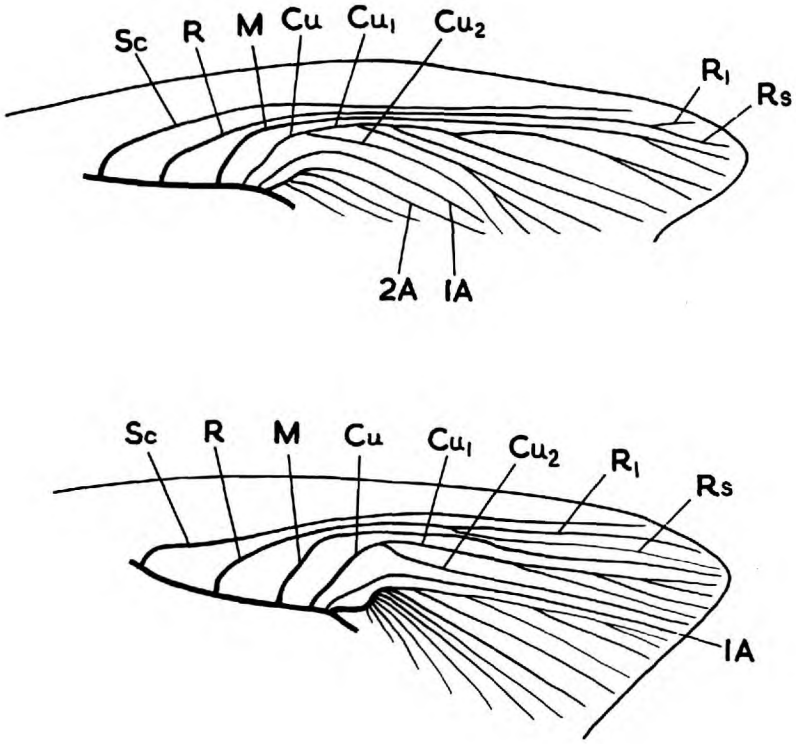


Fig.77. The tracheation of the nymphal wing-pads of Sphodromantis viridis.

common stem.

3. THE VENATION OF THE ADULT WINGS

The account given here of Mantoid wing-venation is largely based on an examination of species belonging to the genera Sphodromantis (Fig. 78), Ameles (Fig. 79), Bolbena, Empusa, and Rivetina. An inspection of the British Museum (Nat. Hist.) Collection suggests that other genera do not differ fundamentally from these.

THE COSTA (C)

This vein is strongly developed along the anterior margin of both pairs of wings. In the fore wing it is often slightly submarginal towards the base of the wing. The costa is convex in the hind wing and often tends to be so in the fore wing.

THE SUBCOSTA (Sc)

The subcosta, which runs behind and parallel to the costa, is unbranched and tends to be concave, especially in the hind wing.

THE RADIUS (R)

This vein runs closely behind the subcosta. In the hind wing it divides near the wing-base into R_1 and R_s, which run parallel to the wing-apex. In the fore wing this bifurcation is much more distal, and in some forms does not take place at all. The radius is convex in the fore wing; in the hind wing R_1 is convex and R_s concave.

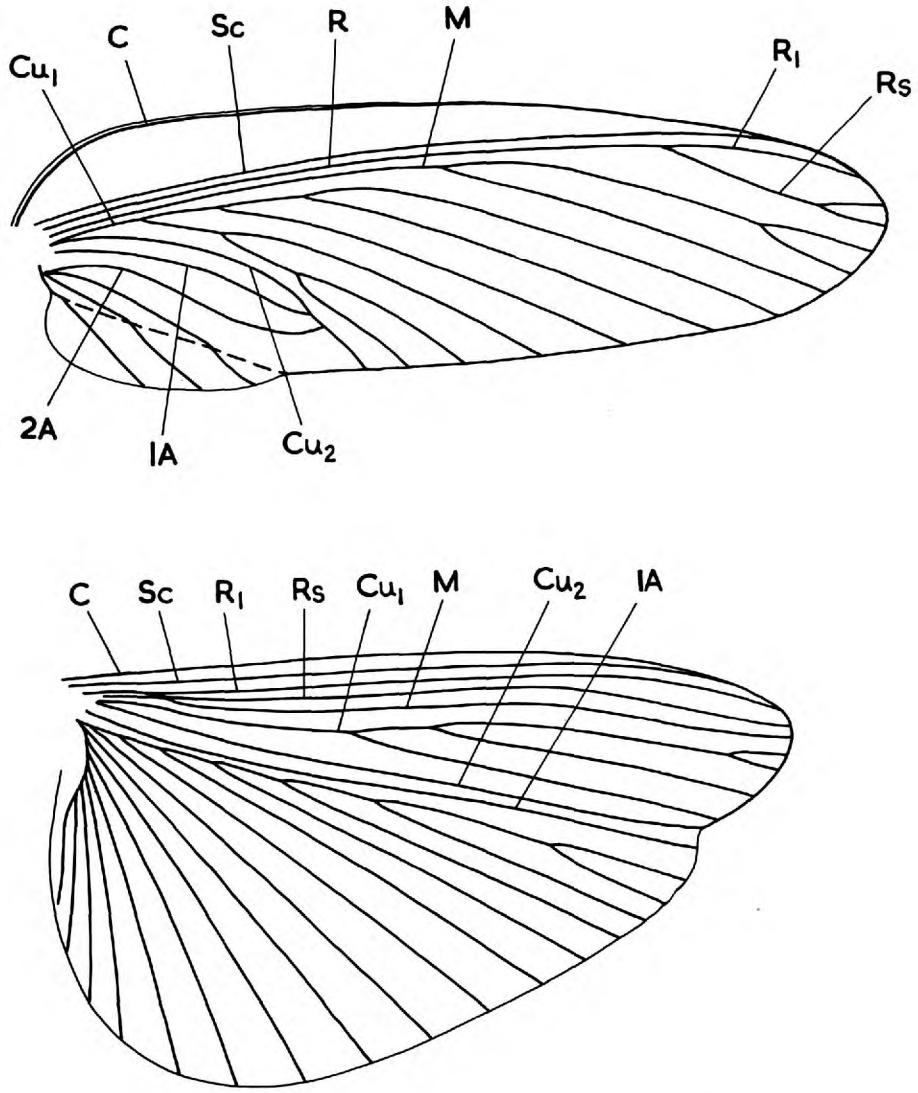


Fig.78. The wings of Sphodromantis viridis.

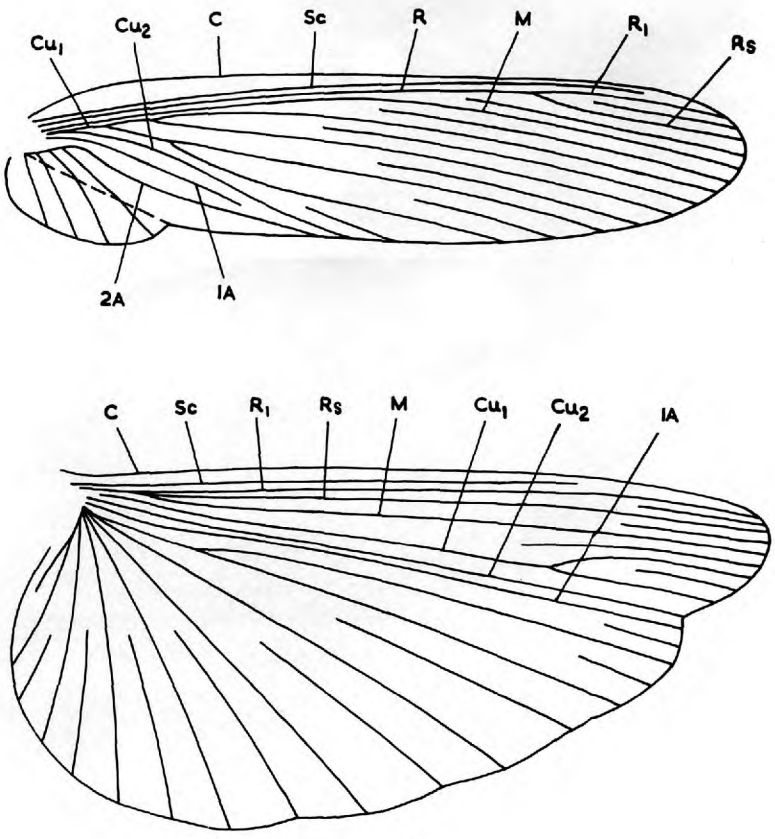


Fig.79. The wings of Ameles heldreichi.

THE MEDIA (M)

The media is situated just posterior to the radius, to which it is basally fused.in most hind wings. It is sometimes a single stem in both pairs of wings, but is frequently two- or three-branched in the fore wing, and occasionally bifurcate in the hind wing. This vein tends to be concave in both pairs of wings.

THE CUBITUS (Cu)

This vein takes the usual Orthopteroid form, being divided at the base into a branched Cu_1 and an undivided Cu_2. In the fore wing Cu_1 is frequently divided into two principal stems, the anterior one giving rise to posterior pectinate branches, and the other to anterior pectinate branches; sometimes Cu_1 is simply bifurcate in the fore wing. In the hind wing Cu_1 is not so profusely branched and is occasionally undivided.

Cu_1 and Cu_2 are convex and concave, respectively, in the hind wing. In the fore wing Cu_2 is concave, but Cu_1 shows no definite convexity or concavity.

THE ANALS

The first anal vein is rather distinct from the remainder in both pairs of wings. In the fore wing it frequently terminates before reaching the wing-margin. No definite homologies can be ascribed to the remaining anal veins, as they normally exceed the supposed ancestral number (three or four, including 1A), and it is impossible to tell in what way the additional veins have arisen. In the fore wing these veins are

simply labelled 1A, 2A, 3A, etc. In the hind wing, however, the position is complicated by the first vein behind 1A bearing a variable number of posterior accessory veins: in the adult wing it is often impossible to tell where these accessory branches are succeeded by distict anal veins. As there is apparently nothing to be gained by applying a nomenclature to these veins, they are not named here.

At the base of the fore wing is a small anal lobe which is folded beneath the remainder of the wing when at rest. This lobe is supported by the distal ends of one or more of the most posterior anal veins. The anal lobe is developed in the usual Orthopterous manner in the hind wing.

1A is normally a convex vein in the fore wing and often tends to be so in the hind wing. There is usually a tendency for the remaining anal veins to be convex also.

XXIV. GENERAL CONCLUSIONS

1. THE SALTATORIA

Although generally conforming to a certain pattern of external appearance, the Saltatoria are by no means a uniform group, and their diversity is particularly apparent in the wings. The latter show their most marked divergence at superfamily level, thus providing the Acridoidea, Tridactyloidea, and Grylloidea, with fairly clear definitions on the basis of their wing-venation alone. In the Tettigonioidea, however, the differences are most evident at family level and this group is impossible to define using the wings only (see p. 146). The most diagnostic features of the wing-venation of the other three superfamilies are set out below.

ACRIDOIDEA

1. The close approximation of the more proximal regions of Sc, R, and M (but not Cu) in the fore wing.
2. The fusion of R and M (at least towards the wing-base) in the hind wing.
3. A tendency towards the reduction of Cu_2 in the fore wing

TRIDACTYLOIDEA

1. The reduction of the fore wings to smooth, sclerotized, lobes.
2. The narrow, well-sclerotized, pre-anal part of the hind wing, forming a band along the anterior edge.

GRYLLOIDEA

1. The development of the harp and associated structures in the stridulatory organ.
2. The close approximation of Sc, R, M, and Cu_1, along the mid-longitudinal line of the fore wing.
3. The division of Cu_1 into two free branches in the hind wing, and the frequent sclerotization or loss of transparency between them.

In spite of the diversity within the group, there are several features of the wings which are common to almost all Saltatorian insects. The most distinctive of these is the submarginal costa of the fore wing: when this vein is well-developed in the present-day Saltatoria it is invariably submarginal, at least towards the base of the wing. The more proximal part of the anterior margin of the fore wing is thus never supported by a primary vein; it is either unsupported or strengthened with a secondary vein. An ambient vein serves this purpose in the Acridoidea, Tettigoniidae, and Schizodactylidae, but in the Prophalangopsidae, Gryllacrididae, and Grylloidea, support is provided only by the tips of the accessory veins in the precostal and costal areas. It is possible that the costa is marginal in some fossil Saltatoria (e.g. fossil Prophalangopsidae and Gryllacrididae), as is normally the case in the Protorthoptera.

Saltatorian wings are commonly modified for the

purpose of stridulation. This occurs in all the superfamilies, though the methods of sound production vary considerably. In the Acridoidea alary sound production is apparently confined to the Acrididae, though it is of course possible that it was also a feature of the fossil family Locustopsidae (especially as the fore wings of these two families are very similar). The usual method of stridulation in the Acrididae is friction between the hind femora and the flexed fore wings. In some cases there are teeth on the inner face of the hind femur; in others the femur merely has a ridge and the teeth are on the fore wing (usually borne by the medial intercalary vein, IM). Occasionally the hind tibial spines are used for the same purpose as the femoral teeth (e.g. Psectrocnemus Henry). Many Acrididae can produce rattling sounds in flight (e.g. Stauroderus scalaris Fischer Waldheim); in these cases it is probable that the hind wings alone are responsible.

In the Tettigonioidea exclusively alary stridulation is found in the Prophalangopsidae and Tettigoniidae. In both cases a tooth-bearing stridulatory rib formed by Cu_2 in one fore wing is rubbed against the hind margin of the other fore wing. In the former family the left and right fore wings are identical and physiologically interchangeable, but in the Tettigoniidae the left fore wing always lies above the right one and the stridulatory rib of the former is always rubbed against the hind margin of the latter. A similar method of stridulation is used in the Grylloidea, though here again the wings are

interchangeable.

Some Tridactylids possess a structure in the fore wing which is probably concerned with stridulation: this is a row of ventral teeth on the distal part of the subcosta. The length of the row varies in different species but is normally less than half the length of the subcosta; it invariably extends to the tip of the wing. The stridulatory function of this structure has apparently not been proven; Carpentier (1936) suggests that the teeth are rubbed against the base of the radius of the hind wing.

Stridulation in the Saltatoria is usually confined to the males, and the wings of this sex are often modified to act as resonators. Thus in the more advanced Acrididae the costal and medial areas of the fore wing are frequently expanded in the male to form enlarged areas of membrane (e.g. Stauroderus scalaris); in some cases other areas are involved (e.g. Brachycrotaphus tryxalicerus Fischer Waldheim, in which the costal and first cubital areas are expanded). In some forms areas of the hind wings are also expanded; an extreme case of this is shown by Hyalopteryx rufipennis Charpentier, in the male hind wings of which the first cubital area is enormously expanded.

In the Tettigoniidae part of the first cubital area of the right fore wing is modified in the male to form the transparent 'mirror', and a similar but less well-developed structure is often found in the left fore wing. The same area

of the male fore wing is used as a resonator in the Grylloidea; in the Gryllidae it has three subdivisions - the 'harp', the 'mirror', and the cordal area (see Fig. 61) - but in the Gryllotalpidae the mirror is rudimentary and the cordal area undeveloped.

In a few cases the female wings are modified in the same way as those of the male. This is the case, for example, in the brachypterous Tettigoniid subfamilies Ephippigerinae, Pycnogastrinae, Bradyporinae, Deracanthinae, and Hetrodinae. In these groups the female usually stridulates, though often to a less extent than the male, and frequently producing a different sound. A number of female Tettigoniids have developed an alary stridulatory apparatus rather different from that of the males. This consists of teeth projecting dorsally from veihs in the posterior part of the anal area of the right fore wing which are rubbed by a downwardly-curved part of the posterior margin of the left fore wing. The apparatus is described in more detail by Fulton (1933). Structures of this sort are found in Scudderia, Conocephalus, and many other genera; they have been observed in operation.

Female stridulation occasionally occurs in the Acrididae. Here, the pegs of the male femur are normally represented in the female by rudimentary teeth or hairs in the same position and similar in number; where there is marked expansion of any of the areas of the male fore wing, the same areas are normal or

only slightly expanded in the female. In spite of these apparent handicaps, however, females are occasionally observed stridulating, and the sound produced is normally loud and typical of the species. For example, a female of Chorthippus bicolor, bred in captivity, chirped almost as frequently and rather more loudly than the males. A microscopical examination of the hind femora of this specimen showed that the rudimentary hairs were no better developed than usual, and their appearance did not suggest that they would be of any use for stridulation. It seems possible, therefore, that well-developed femoral pegs are unnecessary for stridulation, and there is a suggestion that a slightly uneven ridge is quite sufficient.

The remaining features found throughout the Saltatoria are less diagnostic. Ambient veins are common in the Acridoidea and Tettigonioidea, but are not so evident in the Grylloidea, where their function is largely taken over by the tips of accessory veins; ambient veins are not normally found in the Tetrigidae, Tridactylidae, or Gryllacrididae. There is commonly at least a small area of archedictyon in the fore wing, especially towards the wing-base. In most Tettigoniidae and many Acrididae the archedictyon covers the whole of the fore wing, but it is usually much less extensive, and is entirely absent from Tridactylid and Gryllacridid wings.

Accessory and intercalary veins are a very widespread feature of Saltatorian wings. The former are only absent in the Tetrigidae, and the latter only in the Eumastacidae and

Elcanidae; one or other type is thus found in all the families.

It is interesting to note that the anterior media (sensu Lameere, 1922), which is probably absent in most modern orders of insects, is almost certainly present in the Saltatoria. In the Tettigonioidea, moreover, there is a tendency towards the reduction of the posterior media, and in the Gryllacrididae it is very likely that it has been completely lost in most modern forms. It is possible that this is also true of the Grylloidea, but insufficient evidence makes it impossible to draw definite conclusions.

2. THE DICTYOPTERA

Blattoid wings are characterized by the arrangement of the anal veins in the hind wing. The two most anterior of these are typically free and unbranched; the remainder arise principally from two stems, one just behind 2A and the other near the base of the wing. Some of the veins in the centre of the anal fan may be independent of these stems. As a result of this arrangement there are typically three closely parallel, unbranched, veins lying between the anal fan and the pre-anal part of the hind wing, namely Cu_2, 1A, and 2A, and this feature is very characteristic of the Blattoidea. Occasionally, however, Cu_2 has a few terminal branches (e.g. Polyphaga Brulle); rarely it is almost absent (e.g. Anaplecta Burmeister). 1A is sometimes reduced in the more specialized forms (e.g. Blatella Caudell); 2A occasionally becomes basally fused to the branched stem

immediately posterior to it (e.g. Epilampra Burmeister).

Another interesting feature of Blattoid wings is the reduction of the first anal vein in the fore wing. This vein is frequently invisible (e.g. Periplaneta), especially when the anal region of the wing is heavily sclerotized; in no case does it reach the wing-margin. 1A is least reduced in the Pseudomopinae, where it is sometimes as well-developed as the remaining anal veins. The costa is also reduced in the fore wing, being usually represented by a mere thickening of the anterior margin.

The regularly curved cubital furrow of the fore wing provides another diagnostic character; where it reaches the wing-margin the latter is often slightly indented. This furrow separates the anal area from the remainder of the wing.

The fore wings of the Mantoidea are generally characterized by the small anal lobe at the wing-base. The contour of this lobe typically projects from that of the remainder of the wing, and it is generally less sclerotized; the lobe is folded underneath when the wing is flexed. The hind wings are distinctive in having the most anterior part supported by five parallel, unbranched, veins (C, Sc, R_1, R_s, and M), though the media is occasionally bifurcate. This condition is only paralleled in the Phasmida, but in this group the more anterior part of the hind wing is much more heavily sclerotized and serves to protect the anal fan when the wings are flexed (the fore wings being much reduced). The

Mantoidea further are the only insect group possessing both an extensive anal lobe in the hind wing and a well-developed costa along the whole of the anterior margin of the fore wing.

There are a number of venational features which are common to both the Blattoidea and Mantoidea. The characteristically curved Cu_2 of the Blattoid fore wing is commonly found in the Mantoidea, though the cubital furrow is not developed. Cu_1 frequently divides into two main branches in the fore wing, the anterior one giving rise to posterior branches and the other to anterior ones. The arrangement of the veins supporting the anal fan in the Mantoid hind wing is often identical with the arrangement in the Blattoidea, except that in the former group 2A is not separated from the more posterior anals; this resemblance can best be appreciated by comparing Figs. 74 and 78.

3. COMPARISON OF THE SALTATORIA AND DICTYOPTERA

Although bearing a superficial resemblance in general form and texture, the wings of these two groups have few venational features in common. The anal fan is of course common to the hind wings of both groups, and is also found in the Phasmida (and Plecoptera). The cubitus generally bifurcates at or very near the wing-base; Cu_1 is almost always branched and Cu_2 usually undivided. Beyond this there are no important resemblances and the wing-venation provides no strong grounds for considering the two groups to be closely related.

4. KEY TO THE MODERN, WINGED, FAMILIES OF SALTATORIA, BASED ON THEIR WING-VENATION

The most distinctive characters of the wings of the Saltatorian sub-groups can perhaps be best expressed in the form of a key. It should be noted that only characters typical of each group are used, as the key is not of course intended for purposes of identification; forms with reduced or modified venation are not taken into account. The Dictyoptera and Phasmida are included for the sake of completeness.

1. Pre-anal part of the hind wing well-sclerotized for protective purposes and supported by at least four parallel, equally spaced, veins.....PHASMIDA

-. Pre-anal part of the hind wing membranous or, if sclerotized, not containing four parallel, equally spaced, veins.....2

2. Costa (when present) marginal in the fore wing; fore wing usually with a regularly curved Cu_2 without stridulatory teeth and either a small, membranous, anal lobe (folded beneath the flexed wing) or a regularly curved cubital furrow. At least four anal veins in the fore wing

DICTYOPTERA 13

-. Costa (when present) submarginal in the fore wing, at least for part of its length; Cu_2 often bearing stridulatory teeth (in the male) and not regularly curved in the fore wing, or, if regularly curved, fore wing with less than

four anal veins. Fore wing with no anal lobe and the cubital furrow either straight or absent.....SALTATORIA 3

3. Cross-veins of the anal fan of the hind wing confined to a single row.....TRIDACTYLOIDEA (Tridactylidae)

-. Cross-veins of the anal fan diffuse.....4

4. 'Harp' developed in the male fore wing; Cu_1 divided into two free branches in the hind wing and the area between them fuscous.....GRYLLOIDEA 6

-. No 'harp' in the male fore wing; Cu_1 of the hind wing unbranched or the branches fuse again; area Cu_{1a}, when present, colourless in the hind wing.....5

5. Fan of the hind wing limited to the anal area ACRIDOIDEA 7

-. Fan of the hind wing at least including areas Cu_1 and Cu_2 TETTIGONIOIDEA 10

6. Fore wing with a well-developed median fan; 'mirror' and 'cords' present in the male.....Gryllidae

-. Fore wing without a median fan; 'cords' absent and 'mirror' only rudimentary in the male.....Gryllotalpidae

7. Pre-anal part of the hind wing at least equal in area to the anal fan.....Pneumoridae

-. Pre-anal part of the hind wing smaller than the anal fan 8

8. Fore wing less than half the length of the hind wing; hind wing without branched veins.....Tetrigidae

-. Fore wing approximately the same length as the hind wing; hind wing with at least one branched vein.....9

9. Cu_1 branched in the fore wing; hind wing without a posterior ambient vein.....Acrididae

-. Cu_1 unbranched in the fore wing; hind wing with a posterior ambient vein.....Eumastacidae

10. Medial and cubital areas of both pairs of wings much expanded into large foldable fans, forming a coil when the wings are flexed.....Schizodactylidae

-. Medial and cubital areas not expanded in this way.....11

11. Male fore wing without a stridulatory organ; at least four anal veins in the fore wing. Media unbranched Gryllacrididae

-. Male fore wing with a stridulatory organ; less than four anal veins in the fore wing. Media branched.....12

12. Stridulatory apparatus without a mirror; distal part of MP free from the most anterior branch of Cu in the fore wing. R_s free from MA in the hind wing...Prophalangopsidae

-. Stridulatory apparatus with a mirror; distal part of MP

fused to the most anterior part of Cu in the fore wing. R_s partially fused to part of MA in the hind wing

Tettigoniidae

13. Costa feebly developed or absent in the fore wing; fore wing with a cubital furrow. Radius with numerous accessory branches, at least in the fore wing.....BLATTOIDEA

-. Costa strongly developed in the fore wing; fore wing without a cubital furrow. Radius never with more than three branches.....MANTOIDEA

5. PHYLOGENY AND RELATIONSHIPS WITH OTHER ORDERS

While it is fully recognized that it is unsound to base phylogenetic studies on one character alone, the author nevertheless feels that the contribution of the wing morphology to the study of the evolution of the Orthopteroid orders is an important one and should be clearly presented. Moreover, the wings provide a large number of clear-cut, independently varying, structures, and when they become subject to adaptive changes (which is less frequently than with many other anatomical features) it is not apparently of importance which vein is used for any particular purpose. This means that convergence by adaptation is more unlike ly with wing-venation than with many other characters (e.g. mouthparts and, to a less extent, genitalia).

This argument does not of course apply to the general appearance of the wing, but only to the nature of the primary

veins themselves. For example, the fore wings of both the Acrididae and Tettigoniidae are sometimes modified for leaf-mimicry; this adaptation has clearly been evolved quite separately in the two families - it is in fact very likely that in the latter family it has evolved several times. If, however, the venation of the fore wings of a leaf-mimic of one of these families is examined, the arrangement of the primary veins (although modified to resemble leaf-venation) will leave no doubt as to which family is involved, or, if the venation is very reduced, the affiliations of the insect will easily be revealed by the hind wings, which only rarely undergo adaptations of this sort.

The phylogenetic importance of Orthopteroid wings is mainly at family level and higher; there is often little generic or specific variation, and in some groups (e.g. the Mantoidea) even families are sometimes indistinguishable by their wings.

The evolutionary history of the Acridoidea, Tettigonioidea, and Grylloidea, has been adequately discussed in Section VI (pp. 23, 46, and 58, respectively); the Tridactyloidea and Dictyoptera were not included for reasons which are made clear in the introductory remarks to these groups (pp. 102 and 175, respectively). The most likely phylogeny suggested by the wing-venation of the families studied in detail is shown in Fig. 80. The broken lines represent suggested connections of which there is no fossil record; these connections are based

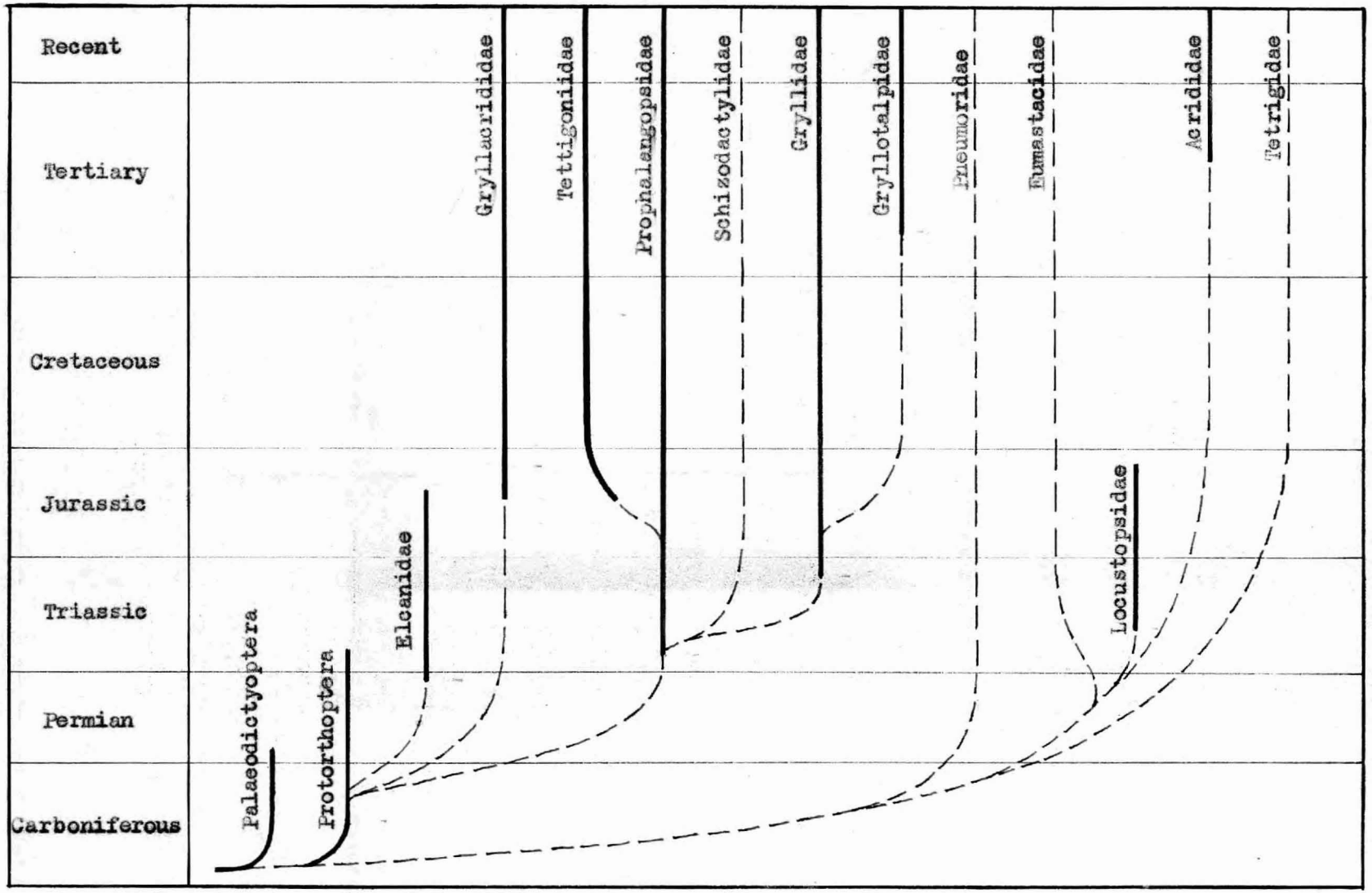


Fig.80. A possible phylogeny of the winged Saltatoria.

on the arguments presented in Section VI (loc. cit.).

It will be seen that this arrangement is in almost complete agreement with modern views on the classification of the Saltatoria (e.g. those of Ander, 1939, and Chopard, 1949). Wing-venation thus provides strong support for these views.

Among the other Orthopteroid orders, the Saltatorian type of wing-venation is perhaps most closely approached by the Plecoptera. The most conspicuous feature which the wings of these orders (and, of course, those of the Dictyoptera and Phasmida) have in common is the anal fan of the hind wing. Though usually relatively smaller than the Saltatorian counterpart, this fan is well-developed in the more primitive Plecopteran hind wings (e.g. Eusthenia Westwood; Pteronarcys Newman), and is supported by a number of anal veins; sometimes area Cu_2 is included in the fan, and there is often a marginal indentation near the tip of 1A or Cu_2. 1A is nearly always unbranched in both pairs of wings, as in the Saltatoria, and this is often true of the other anal veins. In the fore wing there is an anal furrow between Cu_2 and 1A, as in the Acridoidea; it is not, however, used as a hinge. The media is of the simply bifurcate, Acridoid, type. When the radial sector has sufficient branches to show it, it is of the pectinate type; usually, however, it is branched only once or twice. The archedictyon is almost entirely lost in the Plecoptera, there being only traces of it in the wings of a few genera (e.g. Eusthenia).

On the other hand, intercalary veins are not developed.

An important distinctive feature of Plecopteran wing-venation is the basal fusion between R_s and M in the hind wing. The costa is, of course, marginal in both pairs of wings, and there is no modification for stridulation.

There are several venational features which are common to the most primitive Isoptera (i.e. the Mastotermitidae) and the Dictyoptera. Of these the most significant is the cubital furrow of the fore wing, lying along Cu_2; this furrow is, however, relatively much smaller than in the Blattoidea, being confined to the base of the wing. In Mastotermes Froggatt (and a few other primitive genera) the radius branches in a similar fashion to that of the Blattoid fore wing, giving rise to a number of anterior accessory branches. M and Cu are also of the Blattoid type. Mastotermes has a small anal lobe in the hind wing, only part of the anal area being involved; this relatively small size can be only partly due to reduction, as the remainder of the wing has undoubtedly undergone elongation in the evolution of the group. Tillyard (1931) has made further observations on the phylogenetic significance of the Mastotermitidae. The higher Isoptera have a much reduced wing-venation and furnish no additional information.

The remaining Orthopteroid orders have no anal lobe in the hind wing. The wing-venation of the Psocoptera is rather specialized: the subcosta is much reduced, there is only one anal vein, and cross-veins are often completely absent. No deductions of phylogenetic significance can be made from

Psocopteran wing-venation, and this also applies to the reduced wing-venation of the Zoraptera and Embioptera.

6. TAXONOMY

Wing-venation has already been widely used in taxonomical work on the Saltatoria, but hitherto there has been no uniform system of nomenclature available by which legitimate comparisons could be made between the wings of this group and those of other orders or between the various sub-groups of Saltatoria. As most previous attempts to apply the Comstock-Needham vein nomenclature to Saltatorian wings have been confined to isolated species, it has been difficult and often impossible to apply these conclusions to species from other families; furthermore there has been insufficient agreement between the various views put forward for their universal adoption in taxonomic work. It is hoped that this situation will be remedied by the system presented here.

XXV. ACKNOWLEDGEMENTS

I should first like to express my gratitude to Professor J. W. Munro, in whose Department of Imperial College the bulk of the present work was carried out, and to Dr. O. W. Richards, who supervised the work and provided much valuable criticism and advice. Thanks are also due to Dr. R. G. Davies of the same Department, who was responsible for many helpful suggestions and the critical reading of parts of the manuscript.

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XXVI. SUMMARY

1. Comstock and Needham in their work on the homologies of insect wing-veins barely mentioned the wings of the Saltatoria, though briefly describing the tracheation of a few nymphal wing-pads. The author's intention has been to fill in the resulting gap in insect morphology, and thus to facilitate studies on the phylogeny and systematics of the Orthoptera.

2. Over 600 Saltatorian genera were examined. These included representatives of all the winged families and of almost all the winged subfamilies. The wings of over 60 representative species are figured.

3. The criteria used in elucidating the homologies of the veins were those of tracheation, form, position, convexity and concavity, basal articulation, and macrotrichia. Palaeolontological evidence was also studied.

4. From a consideration of these criteria, names based on the Comstock-Needham System are given to the wing-veins and wing-areas of all the winged Saltatorian families. In the case of the Tridactylidae the conclusions are only tentative as no nymphs were available for tracheation studies.

5. A brief account of Dictyopteran wing-venation is also given, the tracheation of representative nymphal wing-pads of the Mantoidea being examined apparently for the first time.

6. The wing morphology of the Saltatoria throws much

light on the phylogeny of the group. The Acridoidea have clearly been quite independent of the remaining Saltatoria in their evolutionary history and have probably had no direct connection with the Protorthoptera. The author suggests that the wing-venation of the Pneumoridae (which is more primitive than that of any other Acridoid family) has been derived with little modification from Palaeodictyoptera of the Stenodictya type.

7. The author demonstrates that the anterior media (sensu Lameere) - probably absent in most insects - is almost certainly present in the Saltatoria.

8. A hypothetical 'standard fossil wing' is constructed which satisfies all the requirements of the wings of a Saltatorian ancestor.

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XXVII. APPENDIX - LIST OF GENERA EXAMINED

PNEUMORIDAE

Bulla Linnaeus

Pneumora Thunberg

Cystocoelia Audinet-Serville

Shortridgea Peringuey

Prostalia Bolivar

LOCUSTOPSIDAE

Triassolocusta Tillyard

Locustopsis Handlirsch

Brodiana Zeuner

Conocephalella Strand

ACRIDIDAE

Catantopinae

Procolpia Stal

Coryacris Rehn

Catreia Uvarov

Agriacris Walker

Colpolopha Stal

Xyleus Gistl

Prionolopha Stal

Rhomalea Fischer

Taeniopoda Stal

Chromacris Walker

Zoniopoda Stal

Aplatacris Scudder

Titanacris Scudder

Lophacris Scudder

Eutropidacris Hebard

Tropidacris Scudder

Dericorys Audinet-Serville

Diponthus Stal

Bactrophora Westwood

Pristocorypha Karsch

Pareuthymia Willemse

Hemiacris Walker

Clonacris Uvarov

Oxya Audinet-Serville

Zulua Ramme

Bermius Stal

Hieroglyphus Krauss

Tristria Stal

Spathosternum Krauss

Oraistes Krauss

Anoxyrrhepes Uvarov

Oxyrrhepes Stal

Afroxyrrhepes Uvarov

Leptacris Walker

Tropidopola Stal

Calamippa Henry

Acanthoxia Bolivar

Leptysmina Giglio-Tos

Oxyblepta Stal

Inusia Giglio-Tos

Tetrataenia Stal

Copiocera Burmeister

Cervidia Stal

Coryphistes Charpentier

Beplessia Sjostedt

Adreppus Sjostedt

Cuparessa Sjostedt

Xiphiola Bolivar

Traulia Stal

Paratraulidia Willemse

Collitera Sjostedt

Adimantus Stal

Zygoclistron Rehn

Homalosaparus Rehn

Pardillana Sjostedt

Caderia Sjostedt

Carinogoniaea Sjostedt

Goniaea Stal

Caproxa Sjostedt

Desertaria Sjostedt

Peakesia Sjostedt

Cirphula Stal

Macrolopholia Sjostedt

Apotropis Brunner

Terpillaria Sjostedt

Stropis Stal

Eumacrotona Sjostedt

Thisoicetrus Brunner

Heteracris Walker

Thisoicetrinus Uvarov

Euprepocnemis Stal

Tylotropidius Stal

Tropidiopsis Bolivar

Choroedocus Bolivar

Bibulus Bolivar

Cataloipus Bolivar

Cyathosternum Bolivar

Amphiprosopia Uvarov

Calliptamus Audinet-Serville

Caloptenopsis Bolivar

Bothrocara Uvarov

Acorypha Krauss

Sphodromerus Stal

Metromerus Uvarov

Sphodronotus Uvarov

Paracaloptenus Bolivar

Brachyxenia Kirby

Calliptamulus Uvarov

Calliptamicus Uvarov

Platyphymus Uvarov

Martinezius Uvarov

Amblyphymus Uvarov

Euryphymus Stal

Aneuryphymus Uvarov

Pachyphymus Uvarov

Macrazelata Sjostedt

Carlippia Sjostedt

Exarna Brunner

Melanoplus Stal

Eirenephilus Ikonnikov

Tonkinacris Carl

Atrachelacris Giglio-Tos

Leiotettix Bruner

Trigonophymus Stal

Osmilia Stal

Staurocleis Uvarov

Cardenius Uvarov

Abracris Walker

Oxycardenius Uvarov

Anthermus Stal

Catantops Schaum

Trichocatantops Uvarov

Orbillus Stal

Anapropacris Uvarov

Eupropacris Walker

Stenocrobylus Gerstaecker

Crobylostenus Ramme

Pirithoicus Uvarov

Allotriusia Karsch

Ischnansis Karsch

Coptacra Stal

Euconptacra Bolivar

Cyphocerastis Karsch

Poecilocerastis Ramme

Apalacris Walker

Bocagella Bolivar

Abisares Stal

Monachidium Audinet-Serville

Antiphon Stal

Teratodes Brulle

Althaemenes Stal

Gerenia Stal

Pachyacris Uvarov

Phyxacra Karny

Acridoderes Bolivar

Anacridoderes Uvarov

Bryophyma Uvarov

Rhytidacris Uvarov

Schistocerca Stal

Anacridium Uvarov

Orthacanthacris Karsch

Ootua Uvarov

Adramita Uvarov

Valanga Uvarov

Patanga Uvarov

Austracris Uvarov

Nomadacris Uvarov

Ornithacris Uvarov

Acanthacris Uvarov

Cyrtacanthacris Walker

Finotina Uvarov

Cristacridium Willemse

Chondracris Uvarov

Paulliniinae

Paulinia Blanchard

Pamphaginae

Buforania Sjostedt

Prionotropis Fieber

Eremopeza Saussure

Ivanotmethis Uvarov

Eremotmethis Uvarov

Tuarega Uvarov

Eremocharis Saussure

Atrichotmethis Uvarov

Asiotmethis Uvarov

Pezotmethis Uvarov

Melanotmethis Uvarov

Tmethis Fieber

Utubius Uvarov

Thrinchus Fischer

Strumiger Zobowsky

Batrachotetrix Burmeister

Tytthotyle Scudder

Aphantotropis Uvarov

Akicera Audinet-Serville

Adephagus Saussure

Lamarckiana Kirby

Porthetis Audinet-Serville

Pyrgomorphinae

Tapesia Bolivar

Maura Stal

Aularches Stal

Taphronota Stal

Rutidoderes Westwood

Phyteumas Bolivar

Phymateus Thunberg

Maphyteus Bolivar

Zonocerus Stal

Poecilocerus Stal

Ochrophlegma Bolivar

Tanita Bolivar

Pyrgomorpha Audinet-Serville

Stenoxyphus Blanchard

Tagasta Bolivar

Atractomorpha Saussure

Ommexechinae

Ommexecha Audinet-Serville

Parossa Bruner

Trigonopteryginae

Trigonopteryx Charpentier

Systella Westwood

Charilainae

Charilaus Stal

Oedipodinae

Aiolopus Fieber

Hilethera Uvarov

Lerinnia Uvarov

Encoptolophus Scudder

Celes Saussure

Homoeopternis Uvarov

Dittopternis Saussure

Pternoscirta Saussure

Heteropternis Stal

Oedaleus Fieber

Gastrimargus Saussure

Locusta Linnaeus

Locustana Uvarov

Hippiscus Saussure

Cratypedes Scudder

Pardalophora Saussure

Xanthippus Saussure

Leprus Saussure

Agymnastus Scudder

Psophus Fieber

Pyrgodera Fischer

Humbe Bolivar

Pycnodictya Stal

Pycnocrania Uvarov

Conistica Saussure

Pycnoderus Uvarov

Chloebora Saussure

Scintharista Saussure

Arphia Stal

Dissosteira Scudder

Spharagemon Scudder

Scirtetica Saussure

Lactista Saussure

Morphacris Walker

Oedipoda Audinet-Serville

Elmisia Dirsh

Psinidia Stal

Metator McNeill

Conozoa Saussure

Derotmema Scudder

Trilophidia Stal

Tmetonota Saussure

Rashidia Uvarov

Pseudotrimerotropis Rehn

Trimerotropis Stal

Circotettix Scudder

Bryodema Fieber

Angaracris Bei-Bienko

Aerochoreutes Rehn

Cosmorrhipis Saussure

Hadrotettix Scudder

Pseudoceles Bolivar

Thalpomena Saussure

Chondronotus Uvarov

Wernerella Karny

Vosseleriana Uvarov

Hyalorrhipis Saussure

Leptopternis Saussure

Helioscirtus Saussure

Sphingonotus Fieber

Iranella Uvarov

Pusana Uvarov

Pternoscirtus Saussure

Acrotylus Fieber

Heliastus Saussure

Pycnostictus Saussure

Qualetta Sjostedt

Xenotettix Uvarov

Anconia Scudder

Coniana Caudell

Cibolacris Hebard

Urnisa Stal

Egnatiella Bolivar

Acridinae

Acrida Linnaeus

Chromacrida Dirsh

Chromotruxalis Dirsh

Yendia Ramme

Acridarachnea Bolivar

Oxytruxalis Dirsh

Truxalis Fabricius

Gelastorhinus Brunner

Gonista Bolivar

Cannula Bolivar

Glyphoclonus Karsch

Parga Walker

Pasiphimus Bolivar

Machaeridia Stal

Wilverthia Bolivar

Paraparga Bolivar

Amphicremna Karsch

Hyalopteryx Charpentier

Oophulella Giglio-Tos

Comacris Bolivar

Paracomacris Karsch

Sumba Bolivar

Duronia Stal

Euprepoptera Uvarov

Orthochtha Karsch

Ceracris Walker

Duroniella Bolivar

Chirista Karsch

Gymnobothrus Bolivar

Phloeoba Bergroth

Holopercna Karsch

Sikkimiana Uvarov

Machaerocera Saussure

Pyrgophloeoba Miller

Xerophloeoba Uvarov

Amblytropidia Stal

Calephorus Fieber

Calephorops Sjostedt

Bootettix Bruner

Brachycrotaphus Krauss

Ochrilidia Stal

Platypternodes Bolivar

Mesopsis Bolivar

Chrysochraon Fischer

Chloealtis Harris

Leva Bolivar

Stenohippus Uvarov

Omocestus Bolivar

Gomphocerippus Roberts

Aeropus Gistl

Myrmeleotettix Bolivar

Stauroderus Bolivar

Chorthippus Fieber

Euchorthippus Tarbinskii

Dociostaurus Fieber

Arcyptera Audinet-Serville

Ramburiella Bolivar

Staurorhectus Giglio-Tos

Eremogryllus Krauss

Heliaula Caudell

Pnorista Stal

Eleutherotheca Karny

Faureia Uvarov

Pseudogmothela Karny

Rhaphotittha Karsch

Aulacobothrus Bolivar

Amphitornus McNeill

Euplectrotettix Bruner

Scyllina Stal

Chortoicetes Brunner

Austroicetes Uvarov

Anaeolopus Uvarov

Caledia Bolivar

Paracinema Fischer

Mecostethus Fieber

Parapleurus Fischer

Eremippus Uvarov

Xerohippus Uvarov

EUMASTACIDAE

Eruciinae

Erucius Stal

Chorotypinae

Chorotypus Serville

Erianthus Stal

Chininae

China Burr

Euschmidtiinae

Euschmidtia Karsch

Cymatopsygma Karsch

TETRIGIDAE

Eugavialidium Hancock

Scelimena Audinet-Serville

Eomorphopus Hancock

Paratettix Bolivar

Euparatettix Hancock

Acrydium Geoffroy

Hedotettix Bolivar

Tettigidea Scudder

TRIDACTYLIDAE

Tridactylinae

Tridactylus Olivier

Rhipipteryginae

Rhipipteryx Audinet-Serville

PROPHALANGOPSIDAE

Haglinae

Hagla Giebel

Prophalangopsinae

Prophalangopsis Martynov

Cyphoderris Uhler

Pamphagopsis Martynov

Zalmona Giebel

GRYLLACRIDIDAE

Palaeorehniinae

Palaeorehnia Cockerell

Jurassobatea Zeuner

Stenopelmatinae

Macrelcana Karny

Gryllacrinae

Gryllacris Audinet-Serville

Paragryllacris Brunner

Licola Walker

Epacra Brunner

ELCANIDAE

Elcana Giebel

TETTIGONIIDAE

Termitidiinae

Termitidium Goldenberg

Ephippigerinae

Ephippiger Berthold

Ephippigerida Bolivar

Uromenus Bolivar

Steropleurus Bolivar

Callicrania Bolivar

Platystolus Bolivar

Praephippigerida Kirby

Baetica Boliva

Pycnogastrinae

Pycnogaster Graells

Bradyporinae

Bradyporus Charpentier

Deracanthinae

Deracantha Fischer

Zichya Bolivar

Hetrodinae

Hetrodes Fischer

Acanthoplus Stal

Cosmoderus Lucus

Enyaliopsis Karsch

Acridoxeninae

Acridoxena White

Pterophyllinae

Pterophylla Kirby

Scopiorus Stal

Thliboscelus Audinet-Serville

Diophanes Stal

Lophaspis Redtenbacher

Pterochroza Audinet-Serville

Tanusia Stal

Ommatoptera Pictet

Mimetica Pictet

Typophyllum Audinet-Serville

Catasparatta Brunner

Cycloptera Audinet-Serville

Paracycloptera Vignon

Pseudophyllinae

Mossula Walker

Sexava Walker

Mustius Stal

Zabalius Bolivar

Cratylus Stal

Pseudophyllus Audinet-Serville

Mioacris Pictet & Saussure

Onomarchus Stal

Brunnea Brunner

Climacoptera Redtenbacher

Cleandrus Stal

Rhomboptera Redtenbacher

Promeca Brunner

Phyllozelus Pictet & Saussure

Stenampyx Karsch

Timanthes Stal

Tympanoptera Pictet & Saussure

Morsimus Stal

Chondrodera Karsch

Cymatomera Schaum

Sathrophyllia Stal

Tegra Walker

Sanaa Walker

Typhoptera Kirby

Xerophyllopteryx Rehn

Tetragonomera Stal

Polyglochin Karsch

Haemodiasma Brunner

Diacanthodis Walker

Anonistus Walker

Pleminia Stal

Lichenochrus Karsch

Acanthodis Audinet-Serville

Platyphyllum Audinet-Serville

Jamaicana Brunner

Meroncidius Audinet-Serville

Movenotus Karsch

Adapantus Karsch

Macrochiton Redtenbacher

Diyllus Stal

Meconeminae

Meconema Audinet-Serville

Mecopodinae

Macrolyristes Vollenkoven

Vetralla Walker

Mecopoda Audinet-Serville

Anoedopoda Karsch

Sthenaropoda Karsch

Pachysmopoda Karsch

Corycus Saussure

Phyllophorinae

Sasima Bolivar

Sasimella Karny

Phyllophora Thunberg

Phyllophorina Karny

Phyllophorella Karny

Siliquofera Bolivar

Tettigoniinae

Tettigonia Linnaeus

Hubbellia Hebard

Glyphonotus Redtenbacher

Amphiestris Fieber

Decticinae

Chlorobalius Tepper

Glampsocleis Fieber

Drymadusa Stein

Capnobotes Scudder

Decticus Audinet-Serville

Montana Zeuner

Pholidoptera Wesmael

Platycleis Fieber

Sphagniana Zeuner

Saginae

Terpandrus Stal

Saga Charpentier

Hemiclonia Kirby

Clonia Stal

Salomoninae

Macroxiphus Pictet

Salomona Blanchard

Agraeciinae

Eubria Stal

Agraecia Audinet-Serville

Nicsara Walker

Copiphorinae

Copiphora Audinet-Serville

Basileus Saussure & Pictet

Exocephala Audinet-Serville

Liostethus Redtenbacher

Pseudorhynchus Audinet-Serville

Pyrgocorypha Stal

Caulopsis Redtenbacher

Conocephaloides Perkins

Homorocoryphus Karny

Conocephalinae

Conocephalus Thunberg

Orchelimum Audinet-Serville

Anisoptera Berthold

Listroscelinae

Phisis Stal

Cerberodon Perty

Hexacentrus Audinet-Serville

Lesina Walker

Tympanophorinae

Tympanophora White

Phaneropterinae

Machima Brunner

Dysonia White

Centrofera Brunner

Paraphidnia Giglio-Tos

Ephippitytha Audinet-Serville

Torbia Walker

Caedicia Stal

Pantolepta Karsch

Acrometopa Fieber

Conchotopoda Karsch

Elimaea Stal

Exora Brunner

Pseudophaneroptera Brunner

Ducetia Stal

Isotima Brunner

Letana Walker

Himerta Brunner

Hyperophora Brunner

Engonia Brunner

Cosmophyllum Blanchard

Poecilogramma Karsch

Scambophyllum Brunner

Tylopsis Fieber

Harposcepa Karsch

Arantia Stal

Acripeza Guerin-Meneville

Zulpha Walker

Leptoderes Audinet-Serville

Tetraconcha Karsch

Drepanophyllum Karsch

Catoptropteryx Karsch

Weissenbornia Karsch

Ancylecha Audinet-Serville

Phygela Stal

Molpa Walker

Tapeina Brunner

Arnobia Stal

Elbenia Stal

Poecilopsyra Dohrn

Psyra Stal

Goetia Karsch

Zeuneria Karsch

Holochlora Stal

Sympaestra Brunner

Tinzeda Walker

Elephantodeta Brunner

Phaneroptera Audinet-Serville

Isopsera Brunner

Pelerinus Bolivar

Terpnistria Stal

Diogena Brunner

Insara Walker

Scudderia Stal

Symmetropleura Brunner

Ceraia Brunner

Pneussia Karsch

Vellea Walker

Chloroscirtus Saussure & Pictet

Microcentrum Scudder

Steirodon Audinet-Serville

Peucestes Stal

Posidippus Stal

Xantia Brunner

Amblycorypha Stal

Sagona Walker

Eurycorypha Stal

Vossia Brunner

Plangia Stal

Anaulocomera Stal

Viadana Walker

Phylloptera Audinet-Serville

Hyperphrona Brunner

Phrixa Stal

Pycnopalpa Audinet-Serville

Topana Walker

Diplophyllus Saussure

Orophus Saussure

Philophyllia Stal

Apoballa Brunner

Dysmorpha Brunner

Prochilinae

Prochilus Brulle

Simoderinae

Simodera Karsch

Moristinae

Narea Walker

SCHIZODACTYLIDAE

Schizodactylus Brulle

GRYLLIDAE

Protogryllinae

Protogryllus Handlirsch

Mesogryllus Handlirsch

Gryllinae

Nemobius Audinet-Serville

Paranemobius Saussure

Brachytrypes Agassiz

Gymnogryllus Saussure

Anurogryllus Saussure

Acheta Fabricius

Gryllus Linnaeus

Gryllulus Uvarov

Gryllodes Saussure

Eneopterinae

Eneoptera Burmeister

Euscyrtus Guerin-Meneville

Heterotrypus Saussure

Madasumma Walker

Orocharis Uhler

Aphonomorphus Rehn

Oecanthinae

Homeogryllus Chopard

Phaeophilacris Walker

Paragryllus Guerin-Meneville

Oecanthus Audinet-Serville

Trigonidiinae

Trigonidium Audinet-Serville

GRYLLOTALPIDAE

Gryllotalpinae

Gryllotalpa Latreille

Neocurtilla Kirby

Scapteriscinae

Scapteriscus Scudder

MANTOIDEA

Ameles Burmeister

Sphodromantis Stal

Bolbena Giglio-Tos

Rivetina Berland & Chopard

Empusa Huebner