FOURTH INTERNATIONAL CONGRESS OF ENTOMOLOGY
ITHACA, AUGUST 1928

VOLUME II

TRANSACTIONS

EDITED BY

K. JORDAN AND W. HORN

ISSUED DECEMBER 1929

VIII + 1037 pages, 183 figures, diagrams
and maps in text, and 12 plates

Communications to be addressed to Dr. K. Jordan,
Zoological Museum, Tring (Herts.), England

PRINTED BY
GOTTFR. PÄTZ, NAUMBURG A/SAALE, WENZELSRING 5.

313

IV. International Congress of Entomology
Ithaca, August 1928
Volume II

Charles P. Alexander

A Comparison of the Systems of Nomenclature that have been applied to the Radial Field of the Wing in the Diptera.

Naumburg a. S. 1929
Buchdruckerei Gottfr. Pätz, Wenzelsring 5

A Comparison of the Systems of Nomenclature that have been applied to the Radial Field of the Wing in the Diptera.

Charles P. Alexander,
Massachusetts Agricultural College, Amherst, Mass., U. S. A.

(With Plates I, II, III.)

The importance of the wing-venation as an aid to a knowledge of the taxonomy and phylogeny of the Diptera is now fully appreciated by all workers on the group. Of all the fields of the wing, the radial, because of its wide extent and relatively numerous veins, would appear to be the most important.

It is only in the two most generalized groups of recent Diptera, the *Tanyderidae* and *Psychodidae*, that the full complement of five radial veins is retained. In all other groups within the order, the field has undergone reduction and the problem of exactly which of the veins have been retained becomes of more than ordinary importance. Edwards (1926: 125—127) discussed the question as it concerns the phylogeny of the Nematocera in the light of the knowledge of the subject then available.

Three distinct systems of terminologies and no fewer than five separate interpretations of the radial veins have been proposed by various workers on the order. The purpose of the present paper is briefly to compare these various interpretations as they apply to the radial field, and, especially, to call wider attention to certain of the more recently proposed suggestions.

One of the earliest, and still one of the most widely used systems of nomenclature of the Dipterous wing is that of Loew (1862)*). This system did not originate with Loew, but was gradually evolved from the work of earlier students of the order, as Meigen and Wiedemann. It received a great impetus from its adoption by Williston (1908) and is still widely used by descriptive Dipterologists in many parts of the World. It is highly unfortunate that Loew selected the Muscoidean type of wing as primitive, with the necessary result that serious complications ensued when families of Diptera with a more complete venation were studied. The Loewian or numerical system still suffices for descriptive purposes, but has a fundamental weakness in its artificiality and the consequent impossibility of determination of strict homologies in very different types or its use as an aid to phylogenetic studies. According to this system, the radial field is made up of the first three longitudinal veins (Plate I, fig. 1). The cells of the wing are the marginal, submarginal and first posterior, but the relative number and position of the first two have been in dispute and have resulted in some confusion in descriptive work (as Philippi, 1865; Osten Sacken, 1869; Williston, 1906). Still more recent workers (as Brunetti, 1912) have continued to modify this system and have unquestionably been influenced in this course by a knowledge of the other and more natural terminologies discussed later.

The second system, the Schinerian, was elaborated by Schiner (1862), chiefly from the earlier work of British and French workers on the order. More recent students, as van der Wulp and Verrall (1901), adopted this terminology and it has thus received wide attention. As was the case with the first-mentioned system, the Schinerian is hampered by its serious artificiality, the continued confusion between true crossveins and deflections of longitudinal veins and the consequent difficulty of obtaining true homologies of parts when a considerable range of venational types are to be considered (Plate I, fig. 2). According to this system, the 1st longitudinal vein of Loew is the subcostal vein, the 2nd longitudinal the radial, the 3rd longitudinal the cubital vein.

A third system, conveniently called the Comstock-Needham or Uniform system, was adapted to the orders of winged insects by Comstock and Needham (1898—1899; Comstock, 1918). Like the two preceding, this was the result of building upon a frame-work laid down by earlier workers along this line, in this case more especially Josef Redtenbacher. This system not only gave to the world a much simpler terminology for the veins and cells of the wings of all winged insects, but, since it was founded on a strict morphological basis, furnished an all-important tool for the study of phylogenetic relationships. The entire radial field was designated by the symbol *R*, with sub-figures to designate the separate veins and cells (Plate I, fig. 3). The Comstock-Needham system is too well known to require further comment, since it has been adopted by the authors of virtually all recent text-books on entomology.

The important studies of Tillyard (1918, 1926), insofar as they affect the Diptera, modify the medial and cubital fields of the wing, but make no changes from the accepted results of Comstock and Needham for the radial field (Plate I, fig. 5).

The first proposal to modify this latter field of the wing in the Diptera was that of Shannon and Bromley (1924), where, from a study of the families of the lower Brachycera, the authors came to the conclusion that the upper branch of the sector, R_{2+3}, is a branched vein, but that the posterior branch, R_3, has been deflected caudad and become permanently fused with the anterior branch of the posterior fork, R_4, to form a fusion R_{3+4}. In the majority of the members of the Brachycera there remains no trace of this basal connection, but in a considerable series of genera and species in many families (as *Leptidae*, *Tabanidae*, *Nemestrinidae*, *Mydaidae*, *Asilidae*, *Therevidae* and *Bombyliidae*), the missing vein is represented either by a complete transverse element, R_3 (*Asilidae: Promachus* and some *Erax; Bombyliidae: Exoprosopa* and some *Anthrax*) or by evident spurs of veins (Plate I, fig. 4).

---

*) Dates in parenthesis refer to the Bibliography at the end of this paper.

A second proposal to modify the radial field of the Diptera is that of the present writer. A consideration of this interpretation, first applied to a single tribe of the *Tipulidae* (Alexander, 1918) and more recently (Alexander, 1927) applied to other families of the Nematocera, furnishes the material for the remainder of the present report. It should be observed that Dr. Tillyard came to almost identical conclusions as a result of his studies on fossil insects (Plate I, fig. 5).

In the most generalized group of living Diptera, the *Tanyderidae*, the radial sector is dichotomously twice branched. In the *Tanyderidae*, as well as the closely allied *Psychodidae*, the four branches of the sector are retained, but in all higher Diptera one or more of these branches have been lost, chiefly by fusion of veins, but in a certain number of cases by atrophy of the elements concerned. The contention of the present theory is that the radial crossvein (r) has never been developed in the Diptera, the element that has been so interpreted in the past being an upward deflection of R_2 that has assumed a transverse position.

The two phenomena that have taken place in the radial field of the Diptera may be briefly discussed as follows:

(1) The cephalization of vein R_2.

In the generalized families of Diptera, as the *Tanyderidae (Eutanyderus wilsoni* Alexander, Plate II, fig. 1), vein R_2 is a fully developed longitudinal vein that lies between and runs parallel to veins R_1 and R_3, attaining the wing-margin as a separate unit. It should be emphasized that in these primitive groups, there is never any indication of the so-called radial crossvein. In all higher families, vein R_2 has swung cephalad and become permanently attached to R_1, forming a short to longer fusion, R_{1+2}. The discovery of a very generalized Tipulid, *Tricyphona protea* Alexander (Plate II, fig. 2), gave the first clue to the true interpretation of this venation (Alexander, 1918). In this insect, R_2 is still a longitudinal element, but the extreme outer end has become permanently attached to R_1. A still more recent discovery, *Tricyphona formosana* Alexander (Plate II, fig. 3), has this backward fusion of R_1 and R_2 still more extensive, forming an intermediate condition that leads to the transverse position of the vein R_2 that is common in the family *Tipulidae* (as *Tricyphona arisana* Alexander, Plate II, fig. 4) and some allied groups and has earlier been interpreted as being the radial (marginal) crossvein. Certain groups of the order that are now known to be very generalized, as the *Ptychopteridae* and *Trichoceridae*, exhibit this feature of the cephalization of R_2, but almost all higher groups have lost the transverse element, R_2, by atrophy. As far as known to the writer, R_2 persists in the Diptera only as high in the scale as the Nemestrinid genus *Nycterimyia* Lichtwardt. The *Ptychopteridae*, although an isolated group, are still placed in the vicinity of the *Tanyderidae* and the occurrence of this phenomenon in the Psychodoidea is of great importance.

(2) The capture of vein R_4 by R_{2+3}.

In the generalized Diptera *(Tanyderidae*, Plate II, fig. 1; *Tricyphona*, spp., Plate II, figs. 2—4), as elsewhere in primitive types in certain of the higher orders of insects, the radial sector is dichotomously twice forked. Except in these scattered lower groups of Diptera, the dichotomy has been lost, the upper fork of the primitive sector being obliterated by the capture of its anterior branch, R_2, by vein R_1, in the manner outlined above (under 1). The lower fork retains its dichotomous nature in a few groups, appearing as a very deep fork, with a correspondingly shortened petiole (Plate II, figs. 2—4). As will be indicated later, the apparent dichotomous nature of the posterior fork of the sector in the lower Brachycera (Plate III, figs. 9, 10) has been brought about secondarily. The dichotomous effect of this fork is lost by the anterior branch, R_4, becoming more intimately attached to and permanently captured by R_{2+3} to form a short to longer fusion, R_{2+3+4}. This apparently unique condition has been brought about in a relatively simple manner by a slight shifting of the veins at the end of the sector. The condition was discussed at some length by *Needham* in his classic study of the venation of the *Tipulidae* (1908: 225—226, fig. 14) and has been considered more superficially by other recent workers on this family.

The first appearance of this phenomenon in the Diptera is in the subfamily *Phlebotominae* of the *Psychodidae* (Plate III, fig. 1), where, because of the lack of the cephalization of vein R_2, the venation of the sector appears pectinate. In the lowermost Brachycera (many *Asilidae, Nemestrinidae* and *Bombyliidae)*, as already discussed under the Shannon-Bromley interpretation, the basal connection of R_4 is still retained as a complete element in many genera *(Asilidae: Pogonosoma, Promachus* (Plate III, fig. 8), *Alcimus, Philodicus, Erax*, etc.; *Nemestrinidae: Exeretoneura, Trichopsidea, Nycterimyia, Cyclopsidea*, etc.; *Bombyliidae: Hyperalonia, Exoprosopa, Pantarbes, Toxophora, Lordotus* and many others). In still other very numerous genera and species, this basal section of R_4 is indicated by a distinct spur (as in *Chrysopila*, Plate III, fig. 9), usually representing the posterior portion of the element, jutting cephalad into cell R_3. Dr. Friedrich Hendel has called my attention to the fact that a trace of the basal section of R_4 even persists as high in the phylogenetic series as the Ortalid genus *Pyrgota*, where its position is indicated by a small spur on R_3, jutting caudad into cell R_3. It should be noted that in all families of the Brachycera in which the free tip of R_4 is retained *(Leptidae* through the *Empididae*, Plate III, figs. 8—10), that this element is permanently connected with vein R_5 by a supernumerary crossvein (s) that is so well established as to simulate the base of vein R_4. A supernumerary crossvein in cell R_4 is found in several generalized Diptera *(Tanyderidae: Nothoderus, Tanyderus, Mischoderus; Tipulidae: Polyangaeus, Heterangaeus)* and its retention in this strategic position in the lower Brachycerous groups in not surprising.

In the accompanying diagrammatic series of figures (Plate II, fig 8, A—J), an attempt has been made to illustrate the two tendencies shown in the radial field of the Diptera. These figures are in all cases based on actual genera and species.

Fig. A. Primitive type of radial sector of the *Tanyderidae.*

Fig. B. The type of *Tricyphona protea;* R_2 longitudinal in position but its tip permanently captured by R_1; a shortening of R_{4+5}.

Fig. C. The type of *Tricyphona formosana;* R_2 oblique in position, a long backward fusion of R_{1+2}; R_{4+5} very short to lacking, cell R_4 thus being sessile to subsessile.

Fig. D. The type found in many Pediciine *Tipulidae.* R_2 subtransverse; R_4 permanently transferred to the upper fork of the sector, R_{2+3}, forming a short R_{2+3+4}.

Fig. E. The type common in Eriopterine and Hexatomine *Tipulidae; Trichoceridae.* R_2 transverse, simulating a crossvein; fusion of R_{2+3+4} extensive.

Fig. F. R_2 atrophied, as in all higher Diptera; R_{2+3+4} extensive.

Fig. G. R_2 atrophied; R_{2+3+4} extensive; R_4 connected with R_5 by a supernumerary crossvein (s) (many of the lower Brachycera, as *Asilidae* and *Bombyliidae).*

Fig. H. R_2 atrophied; basal section of R_4 atrophied, permanently attached to R_5 by a supernumerary crossvein (s) (majority of the lower Brachycera, through the *Empididae).*

Fig. I. R_2 atrophied; R_{4+5} simple, due either to atrophy of the distal section of R_4 (in which case the posterior branch should be interpreted as being R_5) or a fusion of R_4 and R_5 to the wing-margin (in which case the posterior branch should be interpreted as being R_{4+5}) (condition found in the majority of the higher Brachycera, *Dolichopodidae* through the Muscoidea). Exactly the same result is obtained in several Nematocera by a fusion to the wing-margin of elements R_3 and R_4 (as in *Tipulidae: Gonomyia,* subgenus *Lipophleps; Eriocera,* subgenus *Cladolipes).*

Fig. J. R_2 and R_{2+3} atrophied. The single persistent branch of Rs is here interpreted as being R_5, indicating the loss of vein R_4 by atrophy. In some cases, at least, the result is probably obtained by a fusion of veins R_4 and R_5 to the wing-margin. The branches of radius between the anterior branch, R_{1+2}, and the posterior one, R_5, are lost in a variety of ways. In some Nematocera, as the *Blepharoceridae,* R_3 in the most primitive genus, *Edwardsina* (Plate 3, fig. 3) is a long element that extends generally parallel to R_4 and reaches the wing-margin as a separate unit. In all other genera of this family, R_3 is fused backward from the margin with R_{1+2} the element finally disappearing in the axil of the sector (as in the more specialized species of *Bibiocephala).* The main axis of radius in all higher *Blepharoceridae* should be interpreted as being R_{1+2+3} .In the higher *Anisopodidae* and especially the *Mycetophilidae,* R_4 is lost either by atrophy or by fusion with R_3 to the wing-margin. The surviving element, here interpreted as being R_3 alone *(Anisopus,* Plate III, fig. 5) then forms a backward fusion with R_{1+2}, quite as in the *Blepharoceridae.* Very numerous instances of the loss of branches of the sector occur throughout all the higher families and most of the more reduced groups must be studied as separate entities from a strict phylogenetic standpoint.

In the earlier discussion of this interpretation (Alexander, 1927: 57—69), the writer attempted to retain the true radial crossvein (r) in a small group of the *Tipulidae* (Subfamilies *Architipulinae, Tipulinae* and *Cylindrotominae;* Subfamily *Limoniinae,* Tribes *Limoniini* and *Lechriini).* Letters were received from Drs. Tillyard, Mackerras and Tonnoir indicating the improbability of this explanation and offering suggestions by which the venation of all the Diptera were brought into harmony. The original interpretation is shown (Plate II, fig. 5), together with the suggested interpretation which must now be held to be correct (Plate II, fig. 6). It can be seen from this comparison of figures, that in the groups in question, the free tip of Sc_2 is preserved as a distinct element that reaches the margin. The earlier interpretation (Fig. 5) may be brought into harmony with the now accepted view (Fig. 6) by making the following changes of veins in the original paper on this subject (Alexander, 1927, figs. 43—89):

First section of R_1 becomes $Sc_2 + R_1$.
Distal section of R_1 becomes Sc_2 (free tip),
Radial crossvein (r) becomes R_1.
R_2 becomes R_{1+2}.

The groups under consideration present some very puzzling features and the exact interpretation of the radial field may remain in dispute for some time. The diagrams of the wing of *Tanyptera* (Plate II, figs. 5—7) serve to illustrate this problem. Unlike all other members of the Diptera discussed herein, the species of these few subfamilies show no sign of the capture of R_4 by R_{2+3} and the venation has accordingly been interpreted as representing a fusion to the wing-margin of the elements R_4 and R_5. It must be admitted that there is not a bit of evidence that such a fusion has taken place, but there appears to be no other logical way of interpreting this venation. Mr. Hendel *(in litt.* *) is unwilling to accept the interpretation as given (Plate II, figs. 5 or 6), but believes that the terminologies as given herein for the remaining Diptera should be applied to the present groups. This course certainly appears logical since it would then bring all members of the Order into harmony. However, the results of such an application of names in the present groups (Plate II, fig. 7) results in such apparently impossible behavior of some of the elements (as R_2) that the present writer feels reluctant to believe that this explanation is the correct one. More evidence must be forthcoming before the last word will have been said on this particular subject.

Literature cited.

1. Alexander, C. P. 1918 — A new interpretation of the wing-venation of the Pediciine Crane-flies (Tipulidae, Diptera); Ent. News 29, pp. 201—205, pl.
2. id. 1927 — The interpretation of the radial field of the wing in the Nematocerous Diptera, with special reference to the Tipulidae. Proc. Linn. Soc. New South Wales, 52: 42—72, 92 figs.
3. Brunetti, E. 1912 — The Fauna of British India. Diptera Nematocera, pp. 8—16, fig. 3.
4. Comstock, J. H. 1918 — The wings of insects, pp. 1—430, 427 figs., 10 pls.
5. id. and Needham, J. G. 1898—1899 — The wings of insects: Amer. Nat., 32, pp. 43, 81, 231, 237, 240, 243, 249, 253, 256, 335, 413, 420, 423, 561, 769, 903 (1898); 33, pp. 118, 573, 845, 851, 853, 858 (1899).
6. Edwards, F. W. 1926 — The phylogeny of Nematocerous Diptera: a critical review of some recent suggestions. III. Internat. Entomol.-Kongress, 2, pp. 111—130.
7. Loew, H. 1862 — Monographs of the Diptera of North America. Part I. Smithson. Miscell. Coll., vol. 6, pp. xv—xxiii, figs. 3.
8. Needham, J. G. 1908 — Venation of the wings of Tipulidae; 23rd. Rept. State Entomol. N. Y. for 1907, pp. 217—238.
9. Osten Sacken, R. 1869 — Monographs of the Diptera of North America. Part IV. Smithson. Miscell. Coll. No. 219, pp. 31—35, fig.

---

*) Since published: Die Tierwelt Deutschlands, 11. Teil, Zweiflügler oder Diptera, II. Allgemeiner Teil, pp. 1—135, 1928.

10. Philippi, R. A. 1865 — Aufzählung der Chilenischen Dipteren; Verh. zool.-bot. Ges. Wien, 15, pp. 602—617.
11. Schiner, J. R. 1862 — Fauna Austriaca. Die Fliegen (Diptera), 1, pp. x—xv, pl. 2.
12. Shannon, R. C., and Bromley, S. W. 1924 — Radial venation in the Brachycera; Insec. Inscit. Menst., 12, pp. 137—140, pl. 5.
13. Tillyard, R. J. 1919 — The Panorpoid Complex. Part 3. The wing-venation; Proc. Linn. Soc. New South Wales, 44, pp. 533—718.
14. id. 1926 — The Insects of Australia and New Zealand, pp. 333—379.
15. Verrall, G. H. 1901 — Syrphidae of Great Britain. British Flies, 8, pp. 1—691, figs. 24, 84 and 124.
16. Williston, S. W. 1906 — Some common errors in the nomenclature of the Dipterous wing. Psyche, 13, pp. 154—157, fig.
17. id. 1908 — Manual of North American Diptera, Ed. 3, pp. 37—43, figs. 12—20.

EXPLANATION OF THE PLATES.

Symbols:
1—6 = 1st to 6th longitudinal veins (Loew).
A = Anal veins, Analis.
bax = anterior basal crossvein (Loew).
A. I. = Anterior intercalary vein (Loew).
Al. = Alula.
Aux. = Auxiliary vein (Loew).
C = Costa.
Cu = Cubitus (Comstock, Needham).
Cub = Cubitalis (Schiner).
Em = Externomedius or Discalis (Schiner).
h = humeral crossvein.
IM = Internomedius or Posticalis (Schiner).
M = Media (Comstock-Needham).
m = medial crossvein.
Med = Mediastinalis (Schiner).
m-cu = medial-cubital crossvein.
ox = ordinary crossvein (Schiner).
pbx = posterior basal crossvein (Loew).
P. I. = Posterior Intercalary vein (Loew).
px = posterior crossvein (Loew, Schiner).
R = Radius (Comstock-Needham).
Rad = Radialis (Schiner).
r-m = radial-medial crossvein.
Rs = Radial sector.
s = supernumerary crossvein (Alexander).
Sc = Subcosta (Comstock-Needham).
Sub = Subcostalis (Schiner).
sx = small crossvein (Loew).

PLATE I.

Series of wings of Tabanus, sp., to illustrate the following systems of wing-venation:

Fig. 1. Loew (1862).
2. Schiner (1862).
3. Comstock-Needham (1898).
4. Shannon-Bromley (1924).
5. Alexander (1927).

PLATE II.

Fig. 1. Wing of *Eutanyderus wilsoni* Alexander *(Tanyderidae).*
2. Wing of *Tricyphona protea* Alexander *(Tipulidae).*
3. Wing of *Tricyphona formosana* Alexander *(Tipulidae).*
4. Wing of *Tricyphona arisana* Alexander *(Tipulidae).*
5. Diagram of the radial field of *Tanyptera* sp. *(Tipulidae),* with the venation interpreted according to Alexander (1927).
6. The same, as interpreted by Tillyard, Mackerras and Tonnoir *(in litt.)* (1927).
7. The same, as interpreted by Hendel *(in litt.)* (1928).
8. Diagrammatic series of figures, A to J, to show reduction of the Radius in the Diptera.

PLATE III.

Fig. 1. Wing of *Phlebotomus,* sp. *(Psychodidae).*
2. Wing of *Ptychoptera rufocincta* O. S. *(Ptychopteridae).*
3. Wing of *Edwardsina chilensis* Alexander *(Blepharoceridae).*
4. Wing of *Trichocera salmani* Alexander *(Trichoceridae).*
5. Wing of *Anisopus brevis* (Walker) *(Anisopodidae).*
6. Wing of *Pachyneura fasciata* Zetterstedt *(Pachyneuridae).*
7. Wing of *Dixa campbelli* Alexander *(Dixidae).*
8. Wing of *Promachus bastardii* Macquart *(Asilidae).*
9. Wing of *Chrysopila,* sp. *(Leptidae).*
10. Wing of *Empis,* sp. *(Empididae).*

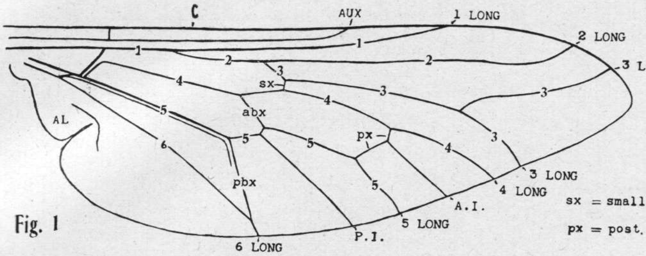

Fig. 1

LOEW (1862)

C = COSTAL AUX = AUXILIARY
1 — 6 LONG = LONGITUDINALS
A. I. = ANT. INTERCALARY
P. I. = POST. INTERCALARY
AL = ALULA
sx = small x-vein abx = ant.bas.x-vein
px = post. x-vein pbx = post.bas.x-vein

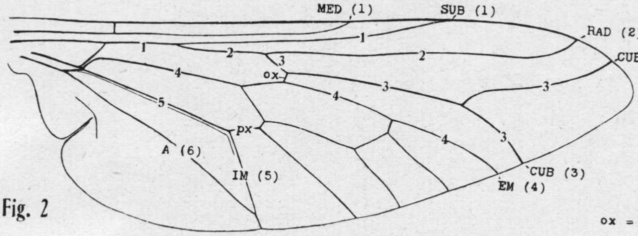

Fig. 2

SCHINER (1862)

C = COSTA
MED = MEDIASTINALIS
SUB = SUBCOSTALIS
RAD = RADIALIS CUB = CUBITALIS
EM = EXTERNOMEDIUS (DISCALIS)
IM = INTERNOMEDIUS (POSTICALIS)
A = ANALIS
ox = ord. x-vein px = post. x-vein

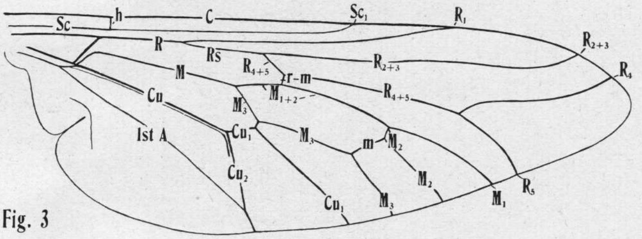

Fig. 3

COMSTOCK-NEEDHAM (1898)

C = Costa
Sc = Subcosta
R = Radius
Rs = Radial Sector
M = Media
Cu = Cubitus
A = Anal

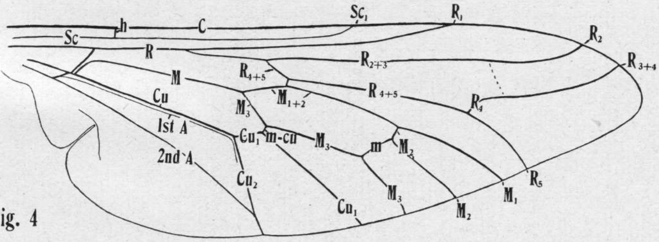

Fig. 4

SHANNON-BROMLEY (1924)

h = humeral x-vein
r-m = radial-medial x-vein
m = medial x-vein
m-cu = medial-cubital x-vein
R_4 = Radius $_4$

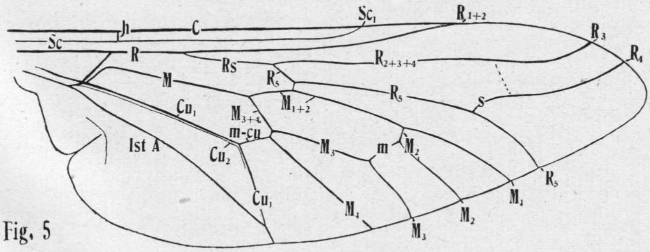

Fig. 5

ALEXANDER (1927)

(MEDIAL AND CUBITAL FIELDS — TILLYARD - 1918)

s = supernumerary x-vein

Alexander, Radial Field of the Wing in the Diptera.

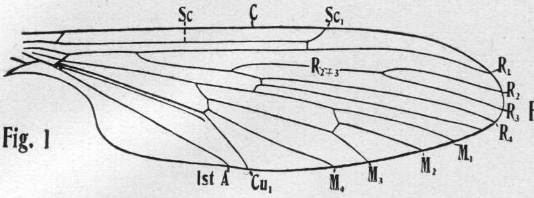
Fig. 1

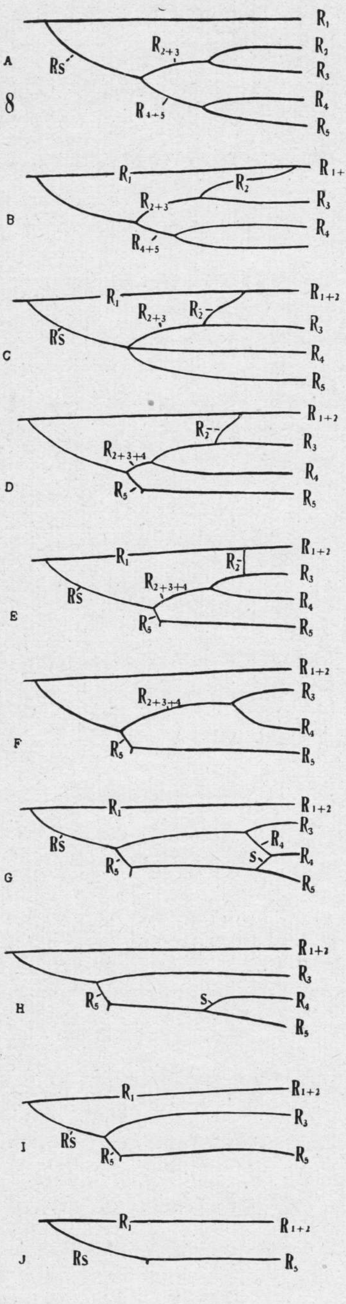
Fig. 8

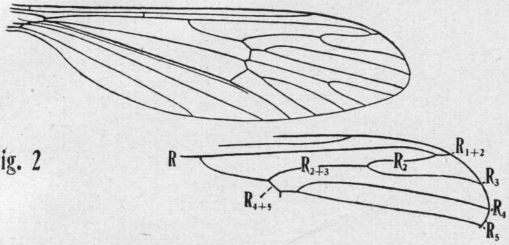
Fig. 2

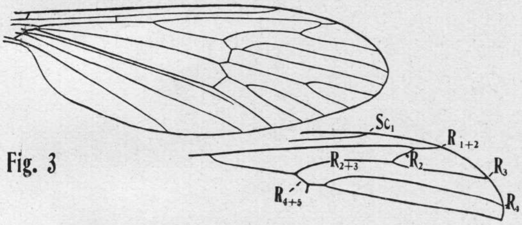
Fig. 3

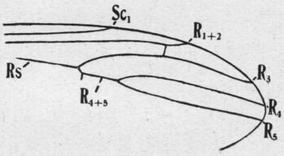
Fig. 4

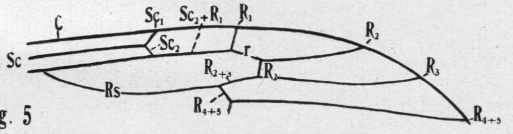
Fig. 5

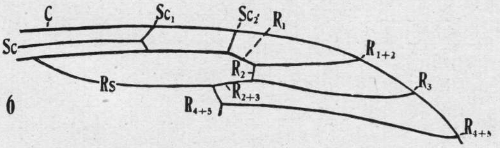
Fig. 6

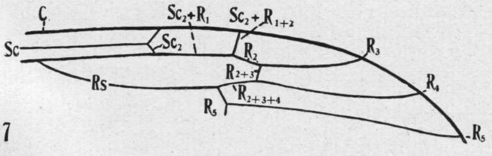
Fig. 7

Alexander, Radial Field of the Wing in the Diptera.

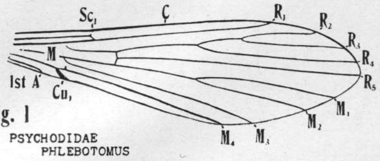

Fig. 1

PSYCHODIDAE
PHLEBOTOMUS

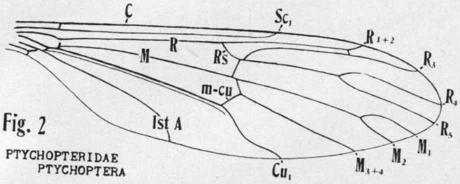

Fig. 2

PTYCHOPTERIDAE
PTYCHOPTERA

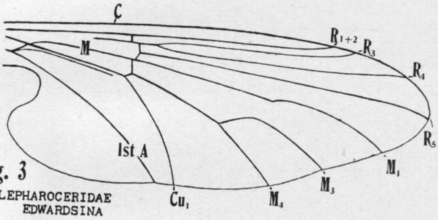

Fig. 3

BLEPHAROCERIDAE
EDWARDSINA

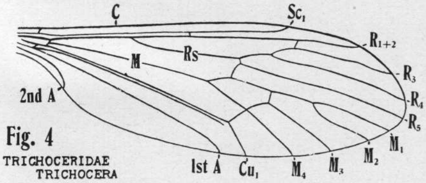

Fig. 4

TRICHOCERIDAE
TRICHOCERA

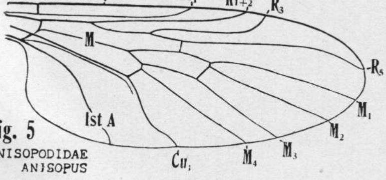

Fig. 5

ANISOPODIDAE
ANISOPUS

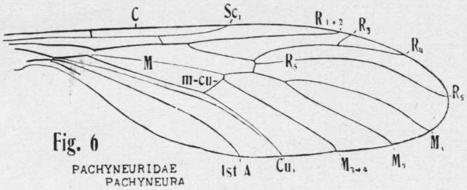

Fig. 6

PACHYNEURIDAE
PACHYNEURA

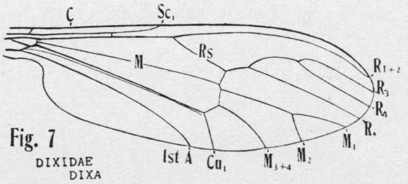

Fig. 7

DIXIDAE
DIXA

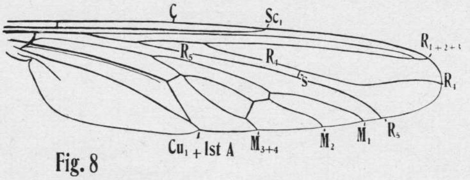

Fig. 8

ASILIDAE
PROMACHUS

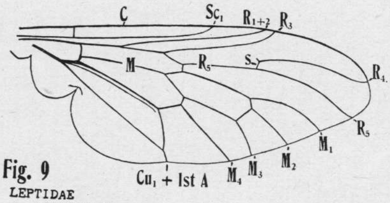

Fig. 9

LEPTIDAE
CHRYSOPILA

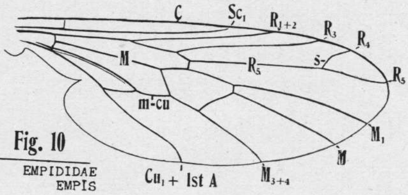

Fig. 10

EMPIDIDAE
EMPIS

Alexander, Radial Field of the Wing in the Diptera.