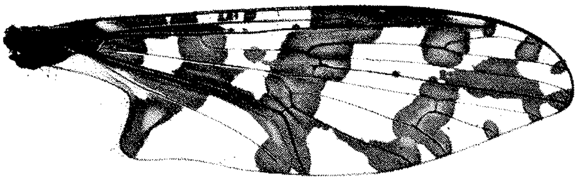
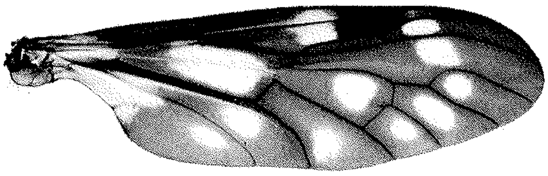
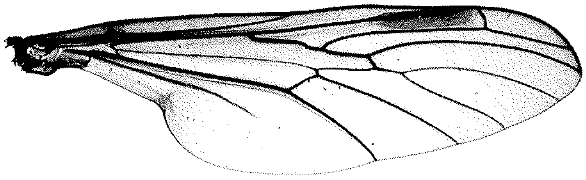
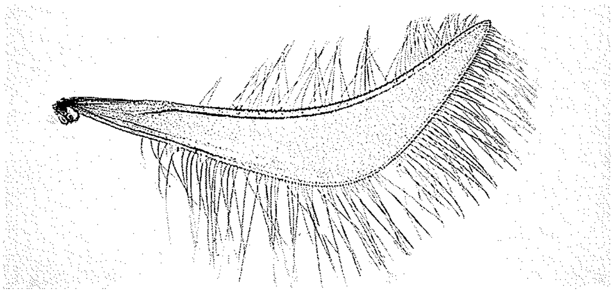
HOMOLOGY OF WING VENATION
OF DIPTERA









Toyohei SAIGUSA
2006

The main purpose of the publication of this booklet is to provide some background knowledge to enable the audience to better understand the oral presentation, "Wing base structure of Diptera" given by T. Saigusa at the symposium, "Morphology and Ultrastructure" at the 6th International Congress of Dipterology held on September 27, 2006 in Fukuoka, Japan.

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The author, Toyohei Saigusa, expresses his cordial thanks to Dr. Bradley Sinclair for his kind suggestions to improve the English texts in this booklet, and to Dr. Mika Sugimoto for her editorial assisitance.

Photographs of wings on cover page: *Protoplasa esakii* Alexander (above, left), *Haruka elegans* Okada (above, right), *Protaxymyia* sp. (below, left) and *Nymphomyia* sp. (below right)

HOMOLOGY OF WING VENATION OF DIPTERA

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双翅目の翅脈相の新解釈と双翅目の起源論への影響

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双翅目の翅脈相の現行の解釈は、M_4脈をCuA_1脈と解釈するか否かという点を除いて、ここ数十年間まったく定説化している。特に、CuA脈の後方、これに近接して走る脈状構造をCuP脈と解釈して、これより後方の２（１）脈をA_1、A_2、(A_1)脈と同定してきた。CuP脈が退行的な溝状構造であって、CuA脈のすぐ後方を、この脈に平行的に走ることと、A脈が２本以下に減少することは、横脈の極端な減少と共に、双翅目の脈相の最も基本的なautapomorphyであり、双翅目の起源を考察する上での、最も重要な形質の一つであると考えられてきた。しかし、これらの翅脈の解釈はまったく間違っていた。演者は、双翅目の翅基部の脈相のパターン、翅脈の凹凸、翅基骨片群との関節状態、trichiation及びtracheationを、双翅目の姉妹群である長翅目との比較のもとに、詳細に検討した結果、次のような新しい解釈に到達した。

１）従来、CuP脈と解釈されていた構造は、全くの二次的構造であって、これは真の翅脈ではない。
２）A_1脈と解釈されていた脈が、真のCuP脈である。
３）A_2脈と解釈されていた脈が、A_1脈である。
４）従来の解釈では、双翅目においては退化してしまったと考えられていたA_3脈（真のA_2脈）は、多くの双翅類に存在する。
５）真のA_3脈も、一部のグループには痕跡的に現れる。
６）従来、MA脈と解釈されていたものは、二次的構造であって、真のMAは双翅目には存在しない。
７）M_4脈またはCuA_1脈と解釈の分かれた脈は、M_4脈と解釈するのが合理的である。従って、CuA脈は分岐せず、CuA_2脈といわれていたものはCuA脈そのものである。
８）M脈とCu脈は、それぞれ基部が判然と残り、これらはdistal median plateと密接な関連を示す。
９）双翅目には従来存在しないと言われていた$cu\text{-}a$, $a_1\text{-}a_2$ crossveinsが存在する。

このような新解釈に基づくと、従来双翅目の起源論で最も重視されていた、CuP脈の退行とCuA脈への接近という、長翅型祖先群からのdeviationは、その意義を失い、むしろCuの前後２分枝は通常の間隔で離れ、かつCuA脈後方に脈状構造が新生される点を祖先群の中に求めていく研究が必要になった。

A new interpretation of wing venation of the order Diptera and its influence on the theory of the origin of the Diptera

Toyohei Saigusa (Biological Laboratory, College of General Education, Kyushu University)

A current interpretation of the wing venation of the order Diptera has been considered as an established theory for this past half century except for the difference in homologizing vein M4, which is considered as vein CuA1 by some authors. This current interpretation is characteristic in identifying a vein–like or furrow-like structure posterior to vein CuA and running close to it as vein CuP, and 2 (or 1) veins posterior to this vein as veins A1 and A2 (vein A1). In addition to the extreme reduction of crossveins, the presence of CuP and reduced number of anal veins (less than3) have been considered the most fundamental autapomorphies in the wing venation of the order Diptera and some of the most important characters in discussing the origin of the Diptera. However, these veins in the current interpretation are misidentified. I reached the following new interpretation based on a detailed morphological study of the pattern of venation, convexity and concavity of veins, basal articulations of veins with the axillary sclerites, the trichiation and tracheation of veins in comparison with those of the order Mecoptera.

1) The structure hitherto interpreted as vein CuP is an utterly secondary structure, and is not a vein.
2) The vein hitherto interpreted as vein A1 is the true vein CuP.
3) The vein hitherto interpreted as vein A2 is the true vein A1.
4) Vein A3 in the current interpretation (true vein A2) hitherto considered to be reduced in the Diptera is retained in many groups of Diptera.
5) True vein A3 appears as a remnant in a few groups of Diptera.
6) The structure which is interpreted as vein MA is a secondary structure, and the true vein MA does not exist in the Diptera.
7) It is reasonable to interpret the vein that has been considered to be either vein M4 or vein CuA1 as vein M4. Consequently, vein CuA does not fork, and the vein hitherto considered to be CuA2 is vein CuA itself.
8) Each of vein M and vein Cu clearly retains its basal portion that is closely associated with the distal median plate.
9) The crossveins cu-a and a1-a2 that are considered to be absent in the Diptera are present.

According to this new interpretation, the reduction of CuP and its approximation to the vein CuA that have been considered to be the most important venational characters in the discussion of the origin of the Diptera loses its significance in this discussion. In research on the origin of Diptera, the stem groups of the Mecoptera-Diptera complex should be searched for the process of appearance of the secondarily developed vein-like structure posterior to vein CuA which runs normally divergent from vein CuP.

[translated from Japanese text in “Abstract of the 49th Annual Meeting of the Entomological Society of Japan”: 70 (1989), the meeting held on October 8 –10, 1989]

A new interpretation of the wing venation of the order Diptera and its influence on the theory of the origin of the Diptera (Insecta: Holometabola)*

Toyohei Saigusa (Biological Laboratory, College of General Education, Kyushu University)

Introduction.

In the order Diptera the wing venation is extremely diversified as in the orders Lepidoptera, Hymenoptera, etc., and it is used as one of the most important taxonomic characters. Several systems on the terminology of the Diptera wing venation have been proposed, and presently many Diptera taxonomists use the Comstock-Needham system that was proposed by Comstock and Needham (1899) who extensively worked on the wing venation throughout the Pterygota under the influence of Redtenbacher (1886). The homology of the wing venation between the Diptera and other Pterygote insect orders has been stabilized since early in the 20th century.

Fig. 1 shows the wing venations with names of veins that have been either proposed or followed by Comostock (1918), Tillyard (1919), Hennig (1954), Rohdendorf (1964), Colless and D. K. McAlpine (1970) in The Insects of Australia, and J. F. McAlpine (1981) in Manual of Nearctic Diptera. In these venations, there is no difference as to one costa (C), one subcosta (Sc) and radius with 5 branches, but number of branches of the media differ among authors, because the 4th branch of the media is interpreted as CuA1, Cu1, M4+CuA1 or M4. However, as to the veins posterior to CuA, CuA2 or Cu1 (or Cu2 of Comstock & Needham) almost all the authors of Diptera taxonomy applied a consistent nomenclature, i.e. the vein-like structure running close to the above-mentioned CuA (of Colless & McAlpine) was homologized with the CuP (or Cu2 of Comstock), and the two (in Tipulidae and Trichoceridae) or one (in other families) vein posterior to the CuP was applied the term anal vein(s). However, Comstock and Needham applied anal vein to all the veins posterior to Cu1 (Cu2 of Comstock and Needham) including the above-mentioned CuP (which they designated as 1st A).

The main purpose of this work is concentrated on the nature and homology of the vein hitherto consistently treated as vein CuP in almost all the recently published works of Diptera taxonomy. One of the distinctive venational features of vein CuP is that it tends to be reduced and more weakly developed than the other main veins, and runs very close to vein CuA (Tillyard, 1919; Rohdendorf, 1964; Colless et McAlpine, 1970; Hennig, 1973; McAlpine, 1981). Even in the generalized groups of Diptera, such as the Tipulidae, Trichoceridae (Fig. 2, A), etc., the vein identified as CuP is developed more weakly than CuA just anterior to it and the vein termed as A1 posterior to CuP, does not reach the wing margin. It is often almost obsolete not only in the higher families of Diptera, such as many Acalyptrate families but also even in some neamtoceran families. The main evidences to homologize this vein as CuP are: 1) this vein is situated just posterior to the vein CuA, 2) it is a concave vein as is the CuP in the generalized venation of the Pterygota, 3) the vein posterior to CuP is a convex vein and is interpreted as the vein A1.

Although almost all the recent Diptera taxonomic works treated this vein as CuP, there were a few authors who were doubtful to this interpretation. Tillyard (1919) observed that the posterior branch of the Cu trachea of a bombyliid species pupa entered into the vein (=A1 of the Bombyliidae) posterior to the CuP not to the latter (Fig.2, B), so that he identified this vein with the posterior branch of the Cu trachea as Cu2+1A in this bombyliid, and he did not give a name to the vein-like structure that he called CuP in other Diptera taxa (it is noteworthy that Tillyard (1919) used term Cu2+1A with a question mark to the vein now identified as A1 in the illustration (p. 617) of *Protoplasa fitchii* wing venation). Rohdendorf (1964) pointed out that CuP (his Cu2) has different optical properties from CuA (his Cu1) when examined under polarized light and interpreted this to mean that the vein must have a different molecular structure from the normal fibrillar cells of the other veins.

The recent very important suggestion on this vein was proposed by Wootton (1979). He pointed out as follows. "Diptera, however, may be an exception. If the orthodox interpretation of the venation is correct, there is no flexion-line associated with CuP, which is often strongly jointed to 1A. Instead a flexion-line, apparently serving the same functions as the claval furrow, lies behind 1A. Further study is necessary to determine whether the position of the claval furrow has changed or whether the cubito-anal veins of flies have habitually been mistinterpreted" (Fig. 2, C).

As a Diptera taxonomist, I have felt a strong incongruity on the nature of the so-called CuP as a wing vein, when observing and illustrating the wings of the Empididae. Finally, when I studied the Triassic fossils of some Mecopteroidea wings discovered at Okuhata, Mine, Yamaguchi Pref., Honshu, Japan, I compared the wings of lower Diptera and Mecoptera in detail in order to study the fossils, and found it difficult to homologize the wing venations, especially of the Cubito-anal field, of the Mecoptera and the Diptera applying the current system of Diptera wing venation including the CuP. This difficulty forced me to apply a different system to this field of the Diptera wings.

Topographic resemblance of wing venation between *Bittacus* and *Trichocera*

In Fig. 3 the venation of the forewing of the genus *Bittacus* (A) of the Mecoptera and that of the genus *Trichocera* (B) of the Diptera are illustrated. The venation of *Bittacus* has one Sc, 5-branched R, 4-branched M, each one Cua and CuP, and three anal veins, and it is almost identical with the basic venational pattern of the Mecoptera. The venation of *Trichocera* is very similar to that of *Bittacus*, and almost identical with the latter except for three branches of the radial sector and the small number of crossveins. Moreover if we consider that CuP of *Trichocera* is not a true vein and interprete veins A1 and A2 of this genus as CuP and A1 as in Fig. 3-B, respectively, it is quite easy to homologize all the veins of the two genera.

The basal areas of the wings of the two genera are shown in Fig.4. In *Bittacus* the stem of M appears externally from the stem of the radius, and it fuses with CuA for a short distance (indicated as "M+CuA"), then it is separated from CuA. After the stem of Cu is divided into CuA and CuP at cu fork, the former is fused with the stem of M for a short distance as stated above, and then it is separated from the stem of M and extends to the wing margin without any contact with other veins. The vein A1 is an independent vein throughout its length, and runs distally along the anal fold, and this vein is connected with the stem of Cu by the cu-a1 crossvein. Both the veins A2 and A3 are independent, and the former is connected with A1 by a1-a2 crossvein. There is a jugal vein in the small jugum.

If we apply the new interpretation to the *Trichocera* wings, the stem of vein M of this genus appears externally near the base of the R stem, and it is anastomosed with the vein CuA for a short distance (indicated as "M+CuA"), then it is separated from the latter. The stem of vein Cu arises from just in front of the anal field, then divided into the CuA and CuP of the new interpretation. The vein CuA is soon anastomosed with the stem of M for a short distance as stated above, and finally it is separated from the M stem. The vein A1 of the new interpretation runs in the rather posterior region of the anal field, and it is connected with the Cu stem by the cu-a crossvein. The veins A2 and A3 are each a very short vein, and the latter is barely recognizable. The small jugal area does not have any jugal vein.

Comparing the venations of the two genera based on the new interpretation, the resemblance between the two genera becomes distinct not only on the pattern (topographic relationship) of the veins on the main area of the wings but also that in the extreme basal area. The resemblance of the wing venation of the two genera almost completely satisfies the first criteria of homology, the resemblance of the topological relationships of the structure with its neighboring structures.

Comparison of convexity and concavity of wing veins between *Bittacus* and *Trichocera*

One of the criteria to homologize the insect wing veins is the convexity and concavity of the veins (Fig. 4). Although this character is often secondarily modified on the distal area of the wings, it is fundamentally constant for each vein at least on the proximal area of the wings. The Cu stem is concave and in both genera the vein CuA is a convex vein. The vein CuP is concave throughout its length in *Bittacus*, and the newly interpreted CuP of *Trichocera* is also concave on its basal and apical parts though it may be more or less convex on the middle part. The structure hitherto interpreted as vein CuP is also concave. In *Bittacus*, veins A1 and A2 are convex. The newly interpreted vein A1 and A2 of the Diptera are convex. The current literature (McAlpine, 1981) pointed out that the structure hitherto treated as CuP is concave and the vein hitherto known as A1 is a convex vein. However, this explanation is not always accurate, and the vein hitherto interpreted as A1 is concave for a considerable length in the primitive nematoceran families, such as Tipulidae and Tanyderidae. Therefore there is no strong evidence against homologizing the vein hitherto known as A1 with the true CuP.

Comparison of cubito-anal area between *Bittacus* and *Trichocera*

The third criterion to support the new interpretation is the positions of the anal veins. The anal veins have a feature that the base of each vein arises independently from the wing base, does not coalesce with each other in Antliophora (Mecoptera+Diptera), and their basal parts are situated on the weakly convex area (anal field) of the posteroproximal area of the wings (Fig. 5, A). In *Trichocera* the vein A1 of the new interpretation (formerly interpreted as A2 in the Tipulidae) runs posterior to the anterior margin of this swelling (Fig.5, B).

The fourth criterion is the position of the claval furrow as already pointed out by Wootton (1979). In order to support the function of the claval furrow, the crossvein cu-a1 connecting the veins Cu and A1 is membranized just before its connection with vein Cu. This weakening is clearly found in *Bittacus* and also in *Trichocera* (Fig. 4) if we homologize the vein hitherto called A1 with the vein CuP according to the new interpretation. As already pointed out by Wootton (1979), the claval furrow runs just posterior to the true CuP that was interpreted as vein A1 in the prevailed system, and consequently the position of the claval furrow is behind vein CuP thoughout the Neoptera.

The articulations between axillary sclerites and bases of veins in *Bittacus* and *Trichocera*

The fifth criterion on the homology of the wing veins is the articulations at the bases of the veins to the axillary sclerites. In the wings of the Neoptera, vein Sc is articulated with the 1st axillary, vein R with the 2nd axillary, vein M arises from the anterior part of the distal median plate, vein Cu from the posterior part of the distal median plate, and all anal veins from the 3rd axillary (Snodgrass, 1935). The wing base structures are illustrated in Fig. 5 for both *Bittacus* and *Trichocera*. The above-mentioned articulations of the veins are clearly observed in the wing base of *Bittacus*. If we apply the new interpretation of veins to the wings of *Trichocera*, the basal articulations of all veins in this genus are identical to those of *Bittacus* as follows: the base of vein M arises from the distal median plate just posterior to the R stem, the Cu stem arises from the posterior part of distal median plate just anterior to the anal swelling, and the three anal veins all arise from the 3rd axillary sclerite. Therefore the new interpretation is strongly supported by the basal articulations of the veins with the wing base sclerites.

The tracheation, trichiation and vein structure in Mecoptera and Dipera

The sixth criterion is the relation between the tracheation and venation of the wings. Although the coincidence between the two structures is sometimes disturbed, particularly apically, tracheation has considerable importance in the identification of the veins. The pupal wing of Diptera belongs to the merotracheate type and pupal tracheation is extremely reduced. However, it is sometimes possible to trace the basal portions of the wing tracheae. As already pointed out, Tillyard (1919) observed the Cu trachea in a bombyliid pupa (Fig. 2, B). I observed the tracheation in the adult wings of an asilid, *Promachus esonicus* (Fig. 7, A), and confirmed that the Cu trachea is bifid, with its anterior and posterior branches entering vein CuA and the newly interpreted CuP, respectively, and the anal trachea enters the newly interpreted short vein A1 that runs on the anterior part of the alula. No trachea is found in the vein hitherto interpreted as CuP. In this asilid, as in the Tillyard's bombyliid, the tracheation and venation are well corresponded with each other in the cubito-anal area.

The seventh criterion is the structure of the veins. The wing vein is formed by the linear thickening of the cuticula of the upper, under or both wing membranes, and the resulting structure is usually semicylindrical with a lumen. The trachea, nerve and haemolymph enter the lumen of the veins. When the vein is reduced or weakened, its cuticula becomes thin. On the other hand, the structure hitherto known as vein CuP has no lumen even when it is strongly developed. Rohdendorf (1964) already pointed out that this structure has different optical properties from other veins. On the other hand, the newly interpreted vein CuP that was hitherto known as vein A1 has a tubular structure when it is strongly developed.

An additional but very suggestive fact is that a concaved vein-like structure similar to the hitherto interpreted CuP appears just after the newly interpreted vein A1 (hitherto known as the vein A2) in some tipulids.

True vein CuP is vein A1 in the traditional terminology in Diptera

As already discussed above in detail, the structure hitherto interpreted as vein CuP in Diptera is not the true vein CuP but a secondary structure that evolved in this order, and the vein hitherto identified as vein A1 is the true vein CuP. This conclusion is strongly supported by all the important criteria or evidences as to the homology of wing veins, and I think there is no evidence to reject this new interpretation.

In Fig. 6, I compare the basal area of wings interpreted by Tillyard (1919), McAlpine (1981) and myself. The veins in black are vein M, and those shaded are vein Cu. Fig. 6a is an illustration by Tillyard. In this figure vein M is fused basally with vein R, then it is separated from R and divided into veins M1-4 and M5. The vein M5 is fused with Cu1 (=CuA). The vein Cu2 (=CuP) is considered as a vein.

Fig. 6-B is an illustration given by McAlpine (1981). In this figure the base of M is not shown, but M is divided into the veins MA and M (=MP), and the vein MA is fused with the R stem. The veins CuA, CuP and A1 are named in the previous system..

Fig. 6-C shows the schema of the basal area of the primitive Diptera wings interpreted by the new system. In this figure vein M has a distinct origin, arising independent from vein R, and partially anastomosed with the true vein CuA, and then it is separated from the latter. Vein Cu is divided into the veins CuA and CuP, and CuP of the previous system is not treated as a vein.

Fig. 6-D shows the schema of the basal area of the higher Diptera interpreted by the new system, and it corresponds to Figs. 6-A and 6-B. In this condition, the stem of vein M is reduced and obsolete, and a furrow-like structure is secondarily developed between veins R and M. This secondary structure is the MA of McAlpine and the stem of M of Tillyard. This secondary structure is not tubular as is a true vein, and does not develop in most weak fliers of the primitive Diptera. The development of this secondary structure is closely associated with the strengthened R kink. The topological relationship of the veins M and Cu in the new interpretation is almost identical with the stage indicated with d of

the Trichoptera wings illustrated by Tillyard (1919) (Fig.6,E). Although he recognized this stage in the Trichoptera, he did not introduce this topography to his archetype venation of the Diptera (p. 619).

Terminology of vein M4.

Apart from the discussion on the vein CuP, I will give a short comment on the vein that was interpreted as M4, CuA1 or M4+CuA1 by various authors (Fig. 7, C). Tillyard (1919) interpreted it as vein M4, not a branch of CuA (his Cu1) as this vein is connected with vein CuA by a crossvein that lacks macrotrichiae (Fig. 7, B). In McAlpine (1981), this vein is identified as CuA1 based on the following evidence: 1) it is a convex vein as CuA, and 2) it often forms the cubital fork with CuA (his CuA2) throughout the Diptera. As to the first evidence, the convexity and concavity of the vein becomes indistinct on the distal area of the wing as stated above. The vein designated as CuA1 by McAlpine is often concave, and even in the Mecoptera, the true vein M4 is often convex. In primitive Nematocera, such as Tipulidae, the apical portion of the M stem often becomes convex. Even the vein M3 of tipulids is often convex if the vein designated as CuA1 by McAlpine becomes convex. So, the convexity and concavity of the vein in question is not a stable criterion for its homology. The formation of the so-called Cu fork is often observed in nematocerous flies with reduced venation. This condition is usually brought by the reduction of the veins situated longitudinally at the middle area of the wing. This condition is probably efficient aerodynamically for the small weak fliers such as cecidomyiids, chironomids, etc.

A stronger disproof against the CuA1 theory is that not only recent taxa but also most fossil forms of Mecopteroidea have a single CuA (Figs. 7, D, E). Some stem groups of Mecopteroidea have branched CuA, but in these taxa the apical portions of veins including the vein M often have many additional branches, and the forking point of CuA is close to the wing margin. I think it is more reasonable to recognize the vein in question vein M4 as interpreted by Tillyard or recent work by Colless and D. K. Mcalpine, not vein CuA1 by J. F. McAlpine.

New interpretation of the wing venation of Diptera

The Diptera wing venation newly interpreted and that based on the hitherto used system are compared in Fig.8. In the new system (Fig.8, A): 1) the R stem has a unique kink on the subbasal area of the wing, 2) the bases of the M and Cu stems are clearly retained, 3) the MA is not recognized, 4) the structure hitherto considered as vein CuP is not a true vein but a secondarily developed cuticular thickening, 5) the vein hitherto considered as veins A1 and A2 are the true veins CuP and true A1, respectively, and 6) the true veins A2 and even A3 are rarely recognized in some nematocerous families.

The new interpretation of Diptera wing venation proposed in this work does not create serious changes to the taxonomy of the extant dipterous families. The homology of the wing veins within extant families of Diptera is already well established, therefore it is quite scientific to use the correct terms here proposed for the veins.

On the other hand, this change of the terminology affects the discussion on the origin of the Diptera among the Mecopteroidea and evolution of Diptera wings including halteres. Fig. 9 shows the ground plan of the Diptera wings interpreted by the new system (Fig.9, A) and the wing venation of the Paratrichoptera (Fig. 9, B). It is noteworthy that there is a great difference between the dotted areas that are the homologous area of the two wings. If we apply the old interpretation to Fig. 9, A, the dotted area becomes very wide, extends to the line connecting the fork of R1 and Rs and the tip of A1 (traditional A2), and does not much differ from that of the Paratrichoptera. This difference indicates that the evolution of Diptera wings are attained by extreme reduction of the anal area that is much wider than hitherto considered.

Rohdendorf (1964) considered that the archetype of the Diptera has vein CuP much weakened and close to the vein CuA. Such inference not only has no means for the discussion but also leads to the wrong inference as to the evolution of the Diptera.

I think that the ancestors of the Diptera probably had proximally narrowed forewings with well-developed vein CuP separated from vein CuA by the usual distance, a sclerotized ridge just posterior to the vein CuA, and the topographic relationship of the basal parts of the veins Cu and M and the anal veins as in the illustration of Tillyard (Fig. 6, E-d), and the freely movable brachypterous hindwings which are not coupled with the forewings. The acquisition of the sclerotized ridge behind CuA and the stage d type of posterior venational topography are important autapomorpies of the Diptera. The evolution of the Diptera was attained by the two-winged condition and the strong costalization of the wing veins. The costalization of the wing veins is much more strongly supported by the new interpretation of the Diptera wings.

The new interpretation and Mecopteroid fossils.

Finally I give a short comment on the effect of the new interpretation to the origin of the Diptera. Many authors support the idea that the order Diptera evolved from the extinct Paratrichoptera, a suborder of the Mecoptera. Therefore in the following lines I check some of the extinct Mecopteroidea (Fig. 10).

Pseudodiptera gallica is said to have a close relationship with the ancestor of the Diptera. However, in the forewing of this species the basal topology of the wing veins is much different from that of the Diptera.

Rieak (1977) treated his *Permotanyderus* and *Chorstotanyderus* as four-winged Diptera and classified them in the suborder Perissoptera of the Diptera. The main reason for his classification is the presence of the R kink. However, the relation of the neighboring veins around the kink is not in accordance with the new interpretation.

On the other hand *Permotipula* that Tillyard (1937) treated as the order Protodiptera seems to have a close relationship to the Diptera. The topographic relationship of the basal parts of the veins M and Cu and anal veins are similar to the ground plan of the Diptera wings of the new interpretation. However, this topography independently evolved not only in the Trichoptera but also in the extant Mecoptera, such as *Bittacus*. Therefore, this topography by itself also does not provide strong evidence for the ancestor of Diptera.

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[*] The original text of this paper in Japanese language was spoken at the 49th Annual Meeting of the Entomological Society of Japan, held on October 8-10, 1989.

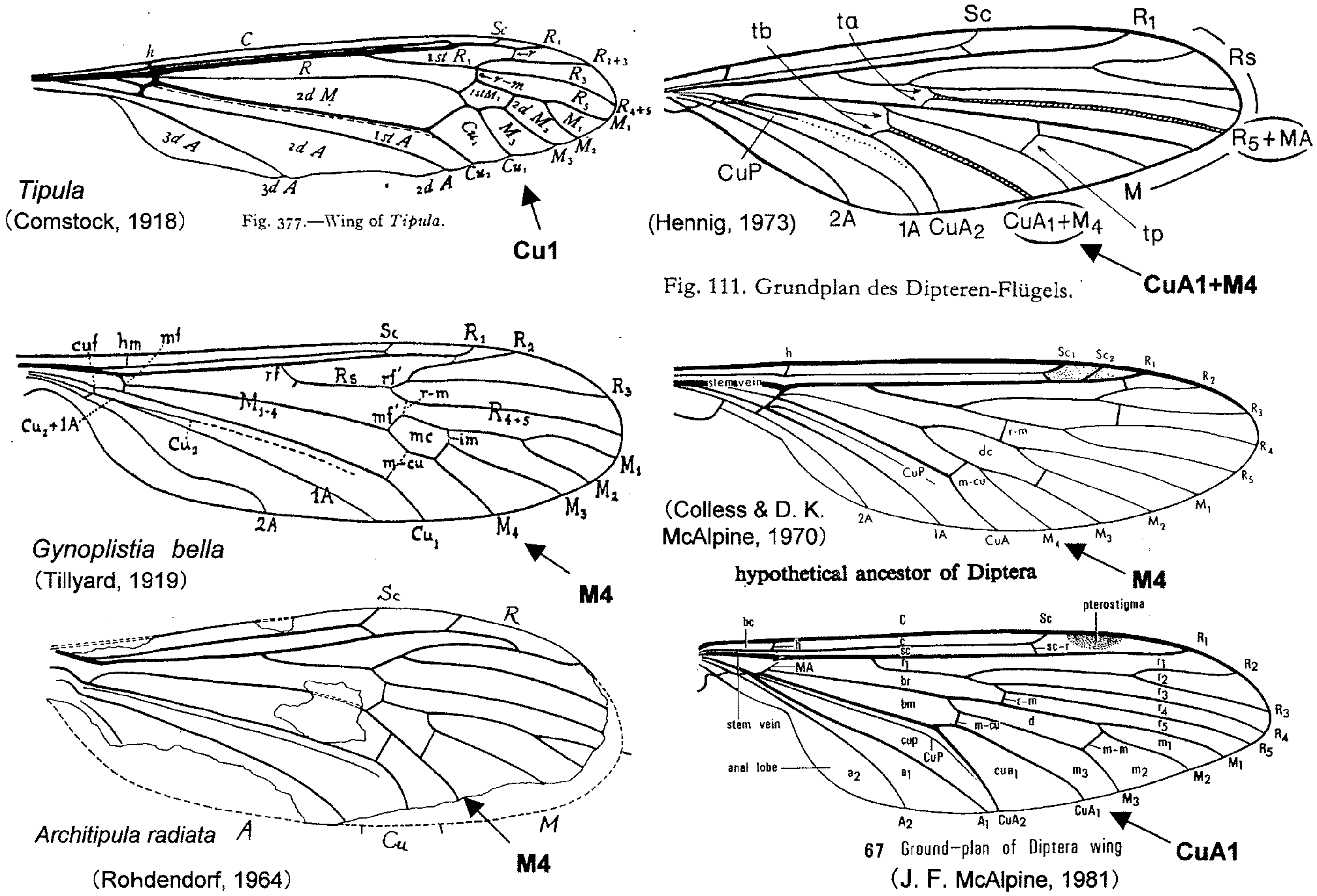
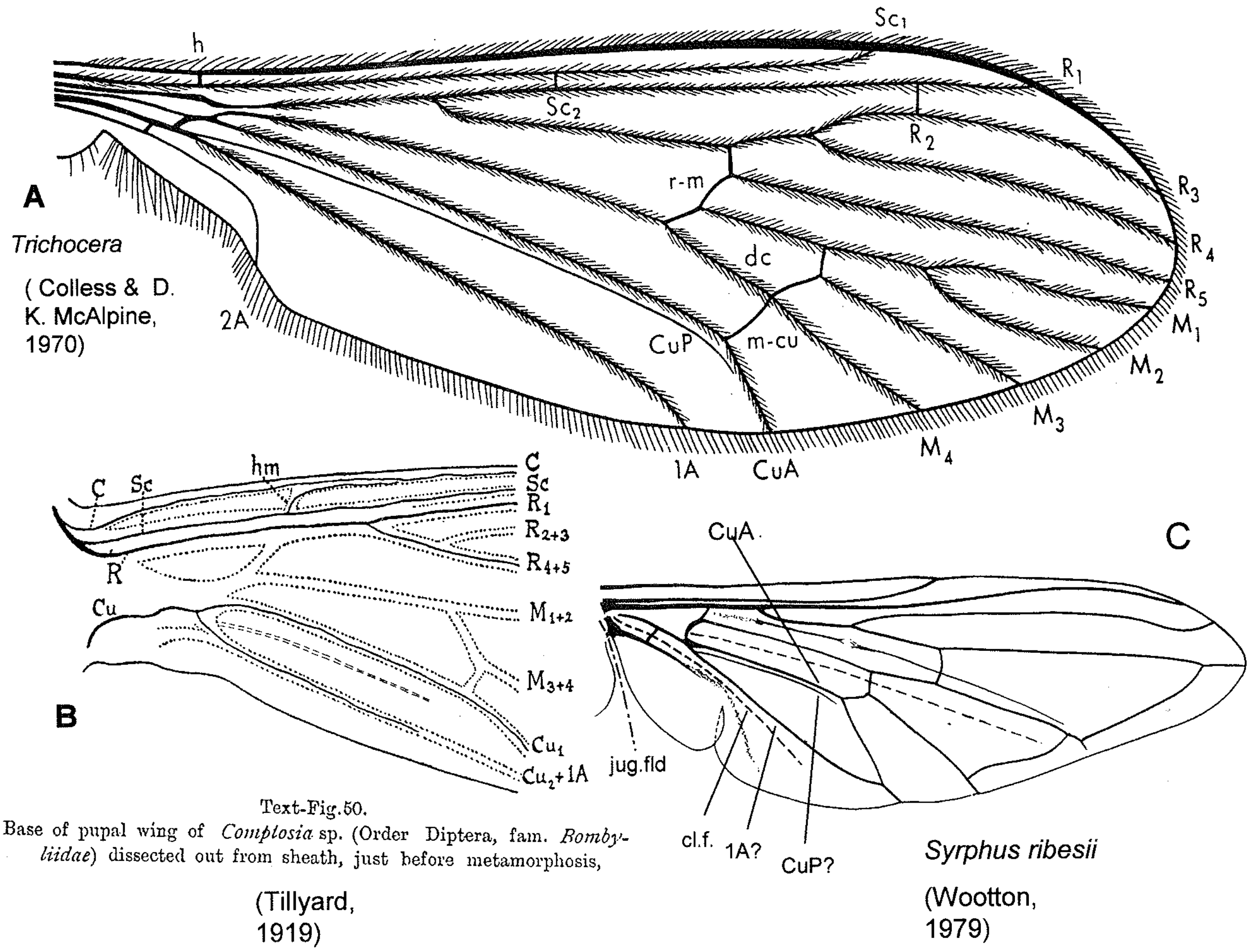


Fig.1. Wing venations of Diptera species.



Trichocera

(Colless & D. K. McAlpine, 1970)

Text-Fig.50.
Base of pupal wing of *Comptosia* sp. (Order Diptera, fam. *Bombyliidae*) dissected out from sheath, just before metamorphosis,

(Tillyard, 1919)

Syrphus ribesii

(Wootton, 1979)

Fig. 2. Wings of Trichoceridae, Bombyliidae and Syrphidae

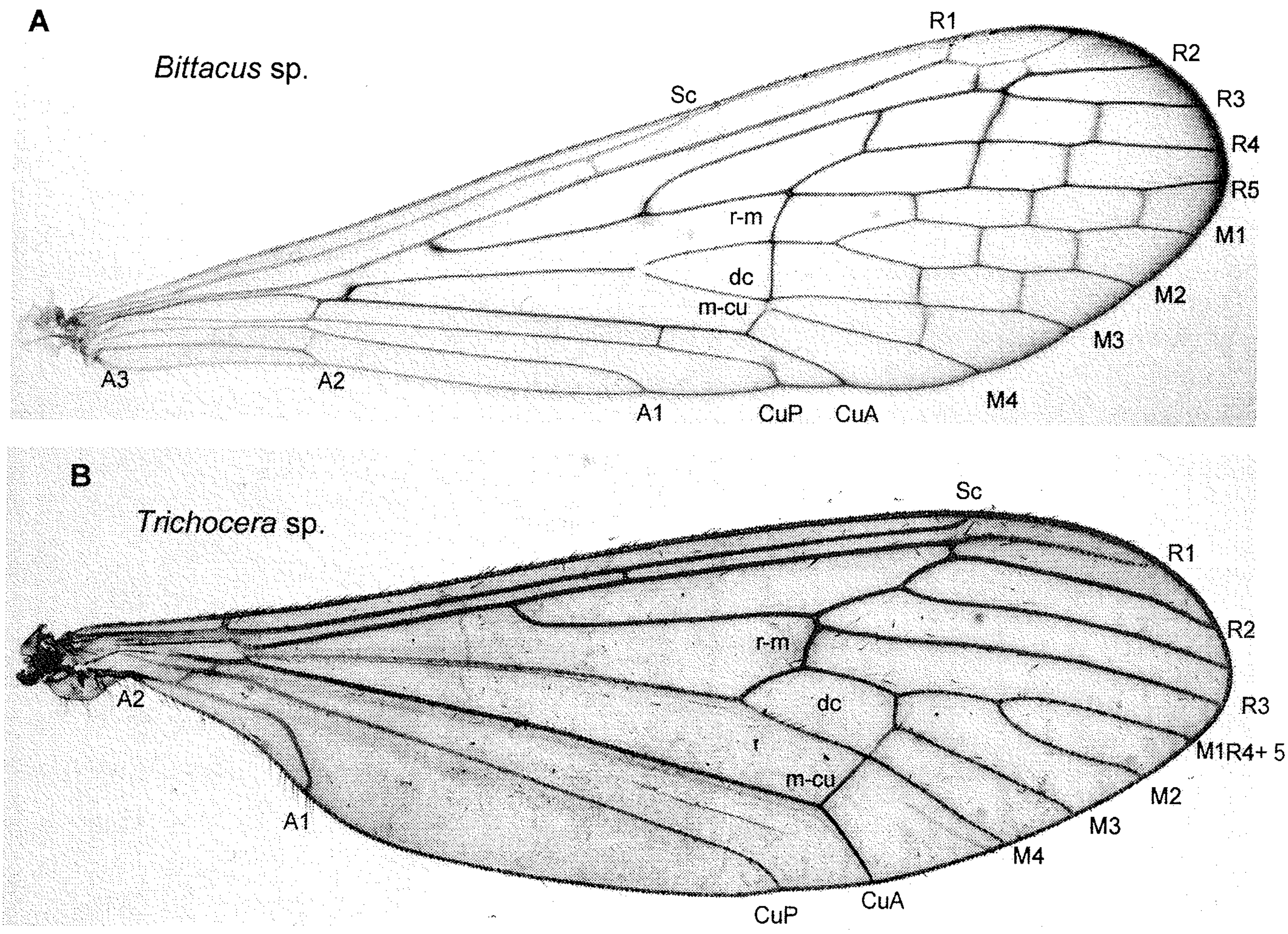


Fig. 3. Wings of *Bittacus* sp. and *Trichocera* sp.

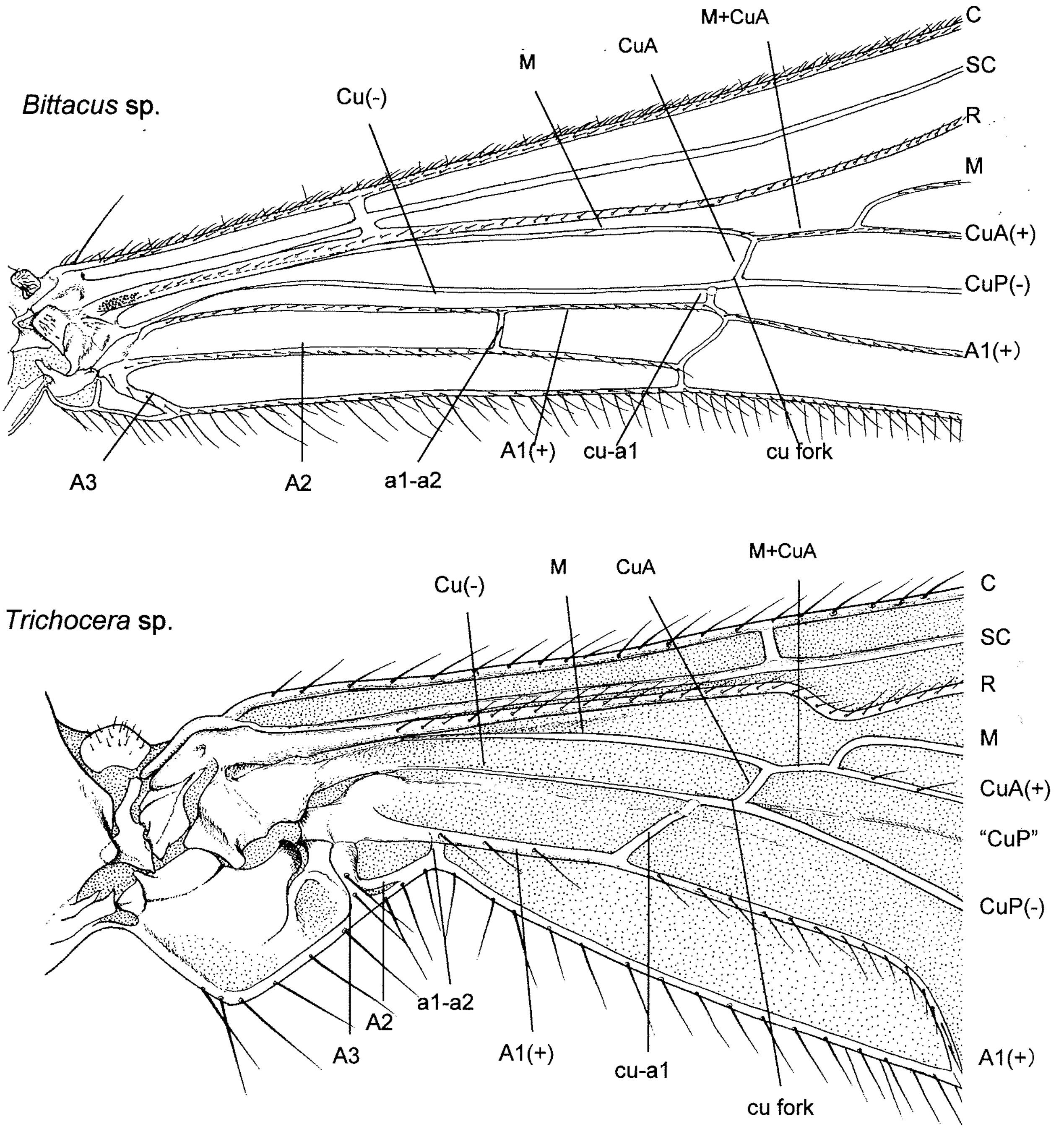


Fig. 4. Basal area of wings of *Bittacus* sp. and *Trichocera* sp.

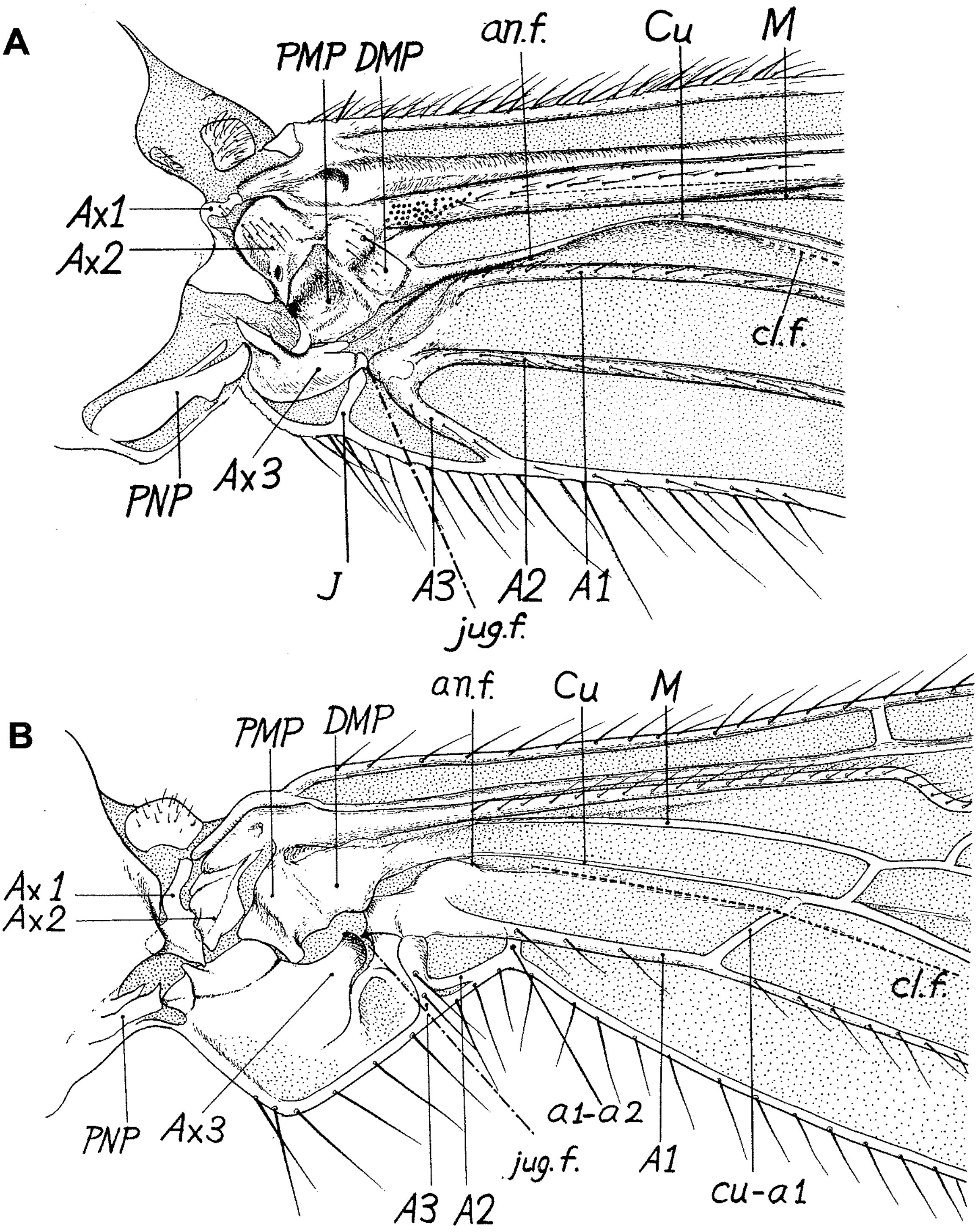
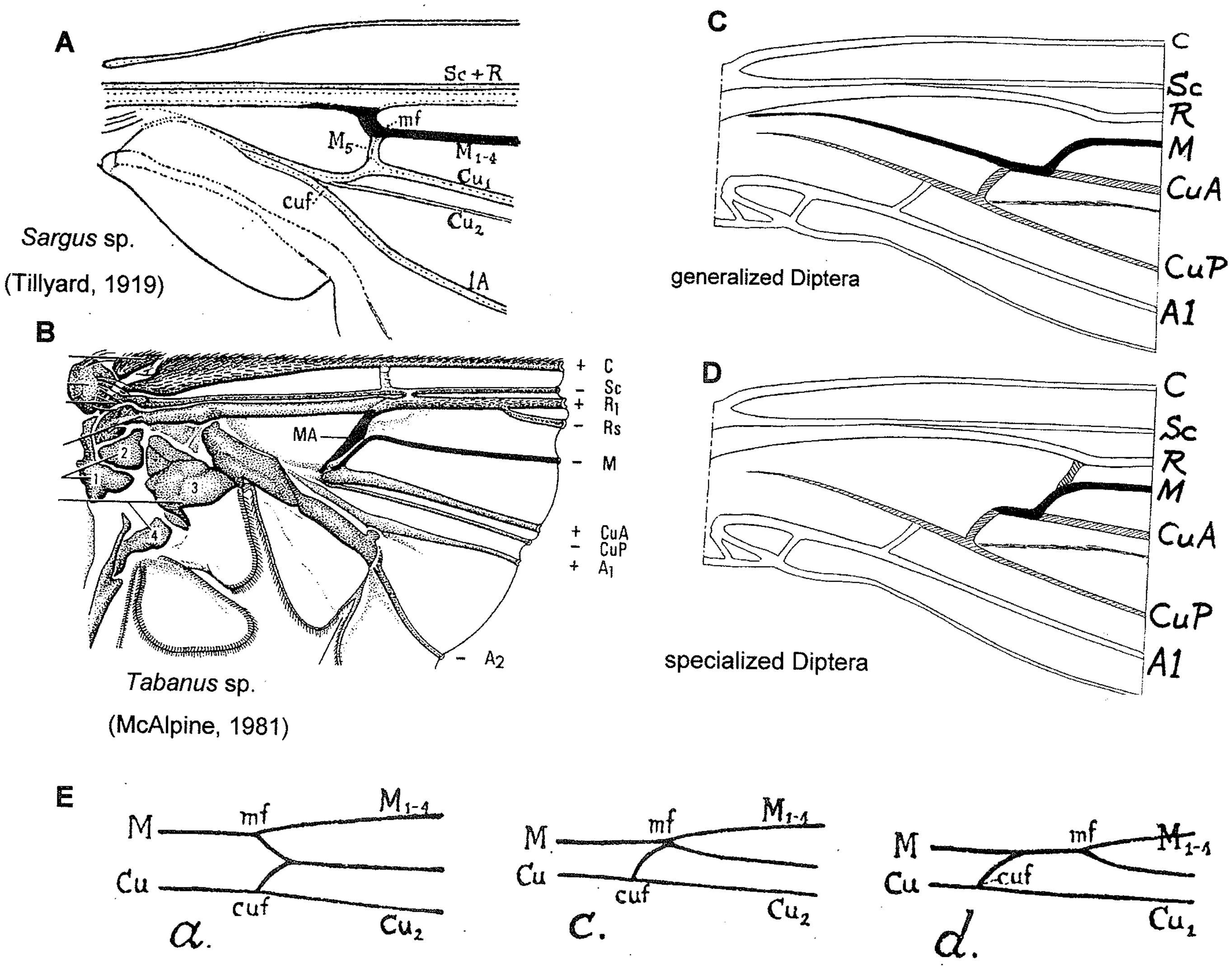


Fig. 5. Wing base structure of *Bittacus* sp. (above) and *Trichocera* sp. (below).



Sargus sp.

(Tillyard, 1919)

Tabanus sp.

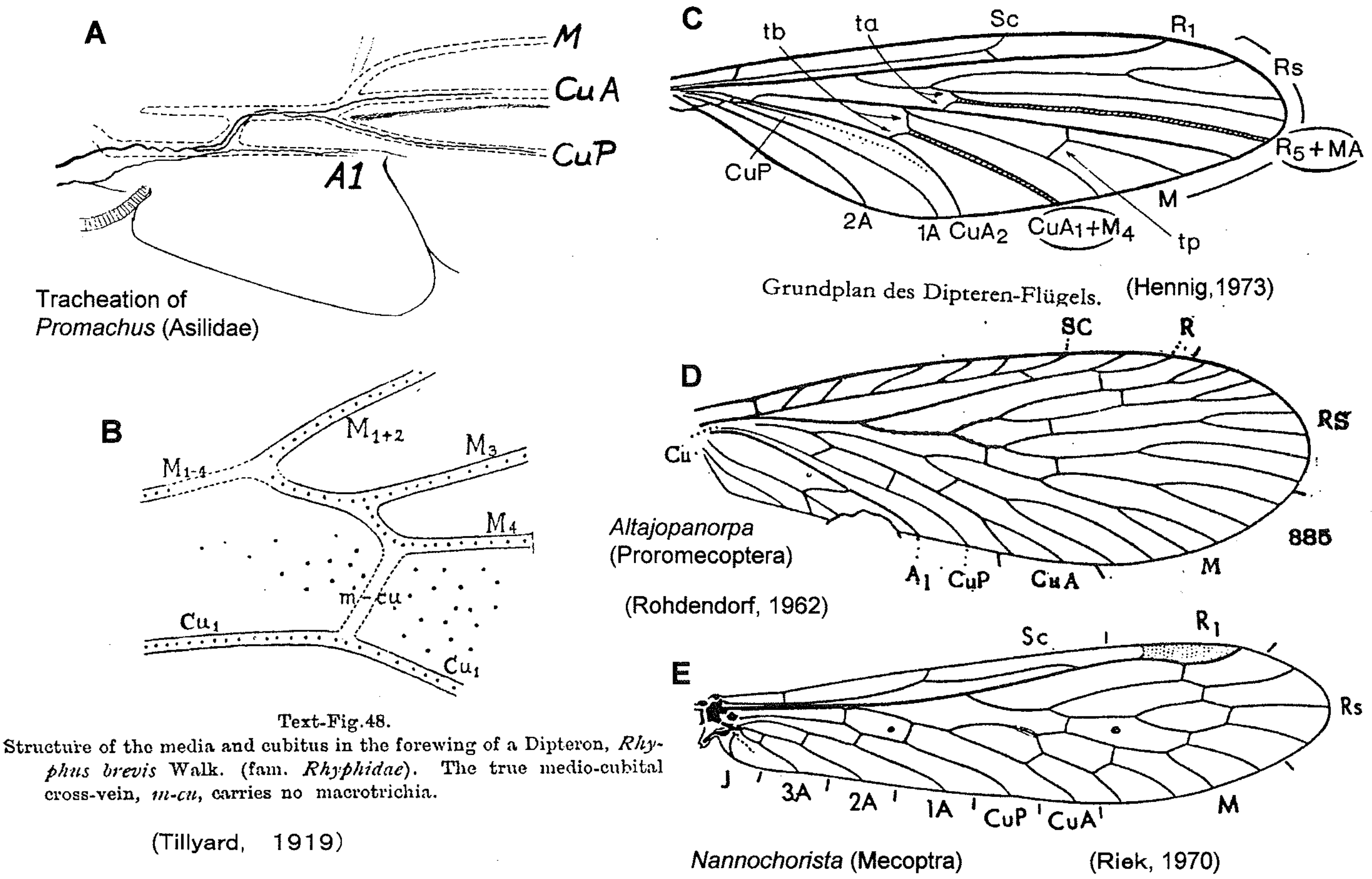
(McAlpine, 1981)

generalized Diptera

specialized Diptera

Stages of fusion of M and Cu. Tillyard (1919)

Fig. 6. Topographic relationship of basal parts of veins M and Cu.



Tracheation of *Promachus* (Asilidae)

Text-Fig.48.
Structure of the media and cubitus in the forewing of a Dipteron, *Rhyphus brevis* Walk. (fam. *Rhyphidae*). The true medio-cubital cross-vein, *m-cu*, carries no macrotrichia.

(Tillyard, 1919)

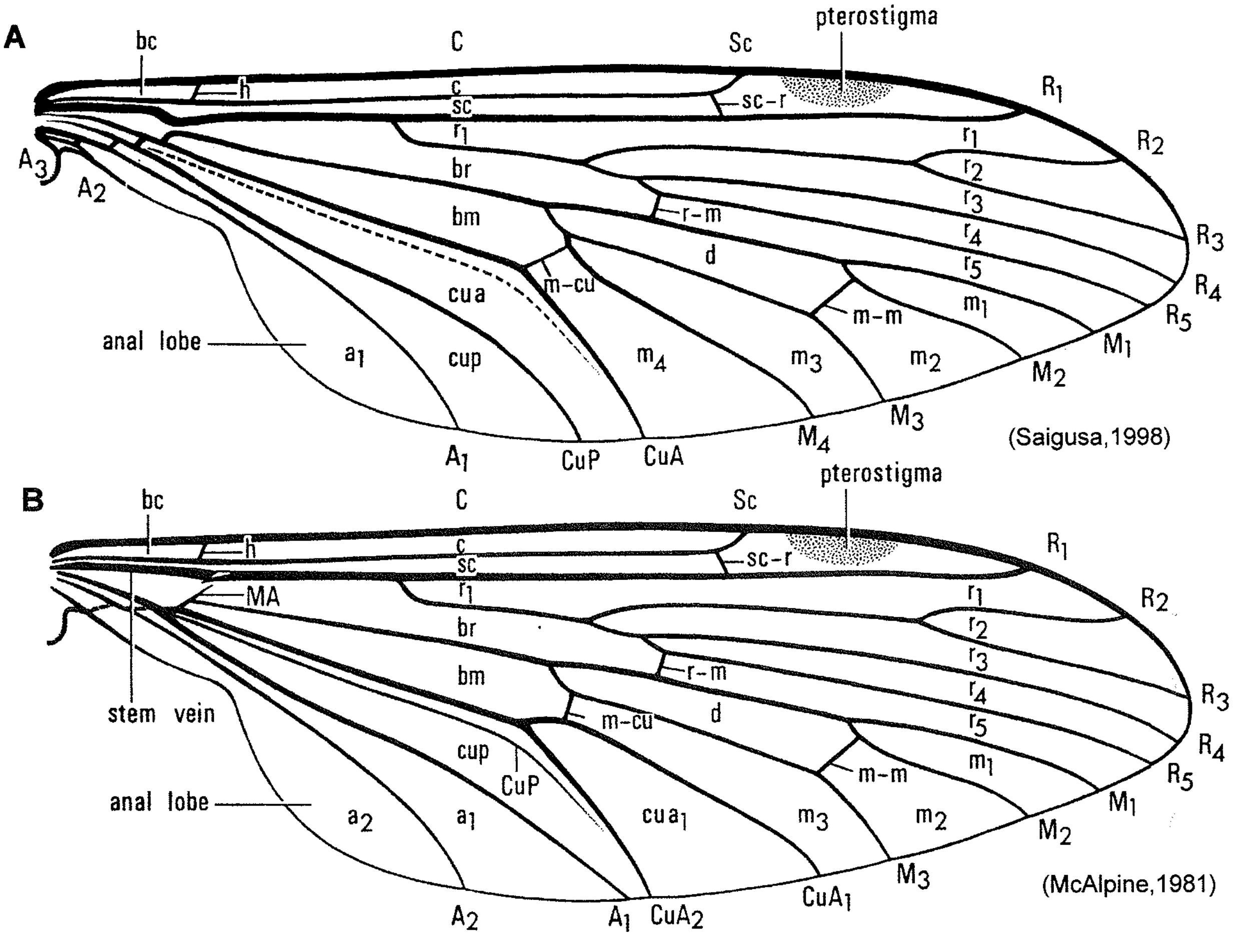
Grundplan des Dipteren-Flügels. (Hennig, 1973)

Altajopanorpa (Proromecoptera)

(Rohdendorf, 1962)

Nannochorista (Mecoptra) (Riek, 1970)

Fig. 7. Tracheation, trichiation and vein CuA.



(Saigusa,1998)

(McAlpine,1981)

Fig. 8. Interpretations of Diptera wing venation: new interpretation (above), and traditional interpretation (below).

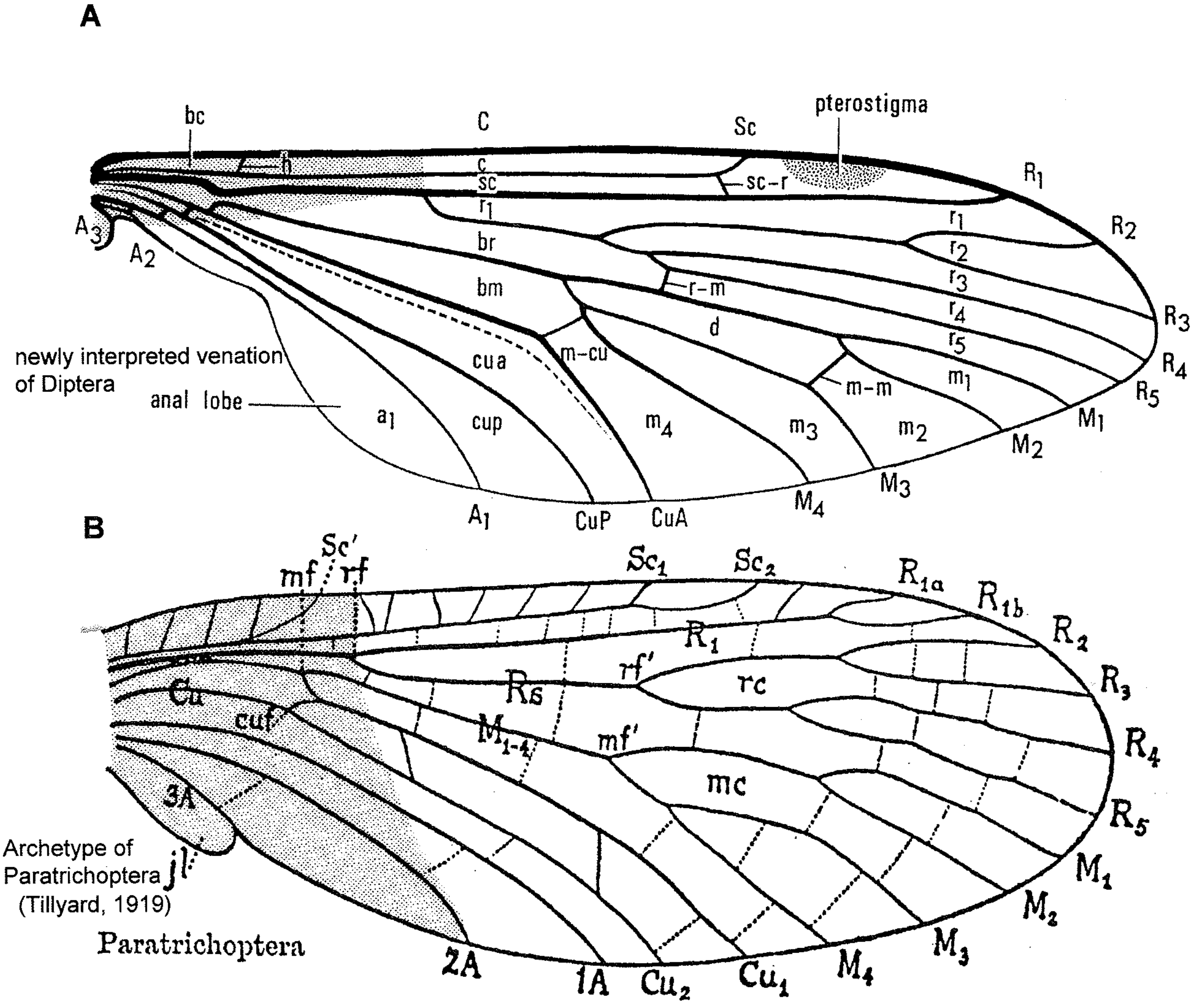
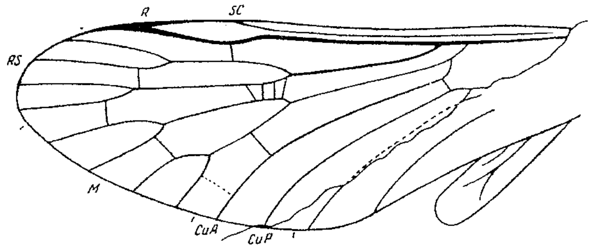
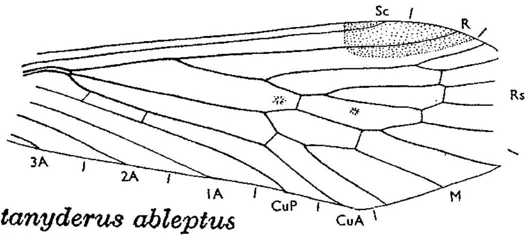


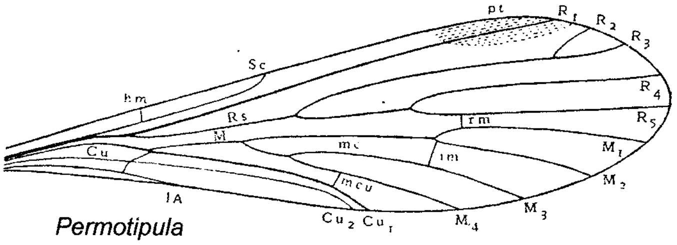
Fig. 9. Reduction of basal area of wings.



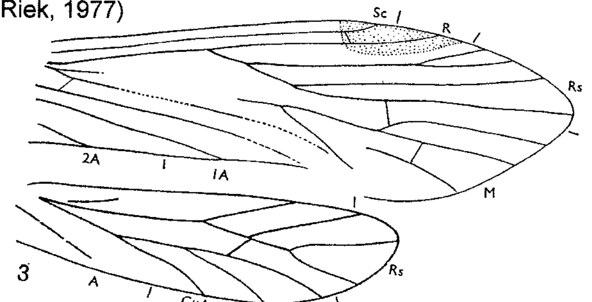
Pseudodiptera gallica Laurentiaux
(Rohdendorf, 1964)



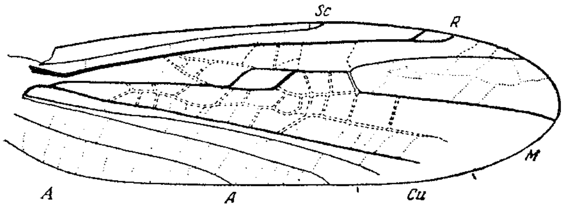
Permotanyderus ableptus
(Riek, 1977)



Permotipula
(Tillyard, 1937)

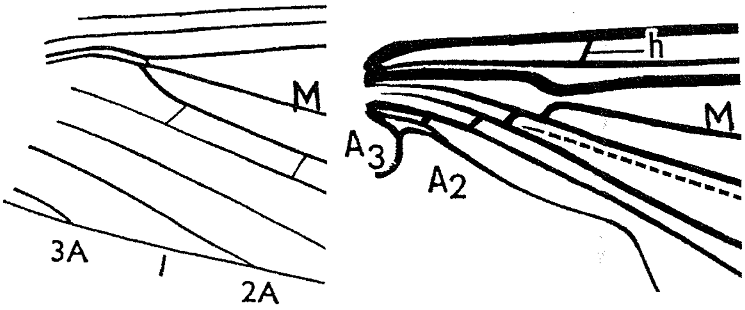


Choristotanyderus nanus (Riek, 1977)



Dictyodiptera multinervis

(Rohdendorf, 1964)



Area around R kink . Left: *Permotanyderus* (Riek,1977). Right: newly interpreted venation

Fig. 10. Fossil Mecopteroids and R kink.

日本昆虫学会第53回大会
第37回日本応用動物昆虫学会大会

（平成5年度　日本農学会大会分科会）

合同大会講演要旨

会場　松本市　信州大学教養部・理学部

会期　1993年4月3日（土）～6日（火）

— 1993 —

日本昆虫学会信越支部

日本応用動物昆虫学会

B 105　双翅目の前翅基部の構造の統一的解釈

三枝豊平（九州大学教養部生物学教室）

双翅目の中胸背板の側縁部，翅基諸骨及び翅脈基部の構造の群間及び双翅目の近縁群との相同性について統一的見解を示す．双翅目の翅基構造の特徴は次の通り．１）Basicostale (humeral plate) は小形化し，C 脈の基部下面に位置する．２）Basisubcostaleは端部が前方に拡大して，この部分で C脈の基部上面に近接し，また基端は Ax 1 前突起先端との密接型の関節を持たない．３）Sc脈は基部近くの下面前方に膜状軟弱部を持つ．４）Basiradiale はその後縁が Ax 2 と細膜状部で分離され，その基端は Ax 1 前突起基部端縁と密接して関節する．５）Clavus基部隆起は顕著，その中央前縁は R脈幹後縁に関節する．６）A1，A2脈間に溝条が発達する．７）Jugal areaは翅脈を欠き，bending cuticleに変わる．なお，Harbach & Knight (1980) のカ科のhumeral plate，Ax2，Ax3，PNWP は，それぞれ basisubcostale，basiradiale の一部，Ax2，PMNWPであり，Ferris (1965) のショウジョウバエ科のhumeral plate，unnamed plate は，それぞれ basisubcostale，basiradiale，McAlpine (1981) の有弁類のbasicostaは basisubcostaleである．諸構造の旧形質と進化方向も論ずる．

B 106　キアシマドアブの外部生殖器と貯精嚢

°永冨　昭・劉　寧五（鹿児島大学農学部）

N. L. Evenhuis（ビショップ博物館）

キアシマドアブ Scenopinus glabrifrons Meigen, 1824 は世界に広く分布し、日本では本州・四国から記録されている。本種の外部生殖器と貯精嚢を紹介する。マドアブ科 Scenopinidae はツルギアブ科 Therevidae と姉妹関係にあり、これは幼虫期における共有子係形質の明確な存在によって確立されている。しかし触角、翅脈、雄外部生殖器、貯精嚢は非常に特化していて、ツルギアブ科と一見して区別できる。

A consistent interpretation of the structure on the forewing base in the order Diptera

Toyohei Saigusa (Biological Laboratory, College of General Education, Kyushu University)

I forward a consistent interpretation on the homology of the structures on the lateral area of the mesonotum, the wingbase sclerites and bases of major wing veins among groups in the order Diptera and between the Diptera and its relatives. Characteristics of the wingbase structures in the Diptera are as follows:

1) The basicostale (humeral plate) is reduced in size, and located below the base of vein C.
2) The anterior portion of basisubcostale is enlarged and approximated on this area to the upper portion of the base of vein C, and the proximal end of the basisubcostale lacks a close articulation with the apex of the anterior process of the first axillary plate.
3) Vein Sc has a weakened membranous area anteroventrally near its base.
4) The basiradiale is separated from the second axillary plate by a narrow membranous area along its posterior margin, and the proximal end of the basiradiale is closely articulated with the distal margin of the basal portion of the anterior process of the first axillary plate.
5) The basal swelling of the clavus is distinct, and the middle portion of the anterior margin is articulated with the posterior margin of the stem of vein R.
6) A distinct suture is developed between the veins A1 and A2.
7) The jugal area lacks any vein, and it is modified into bending cuticle.

The humeral plate, second axillary plate, third axillary plate and posterior notal wing process of the family Culicidae in Harback and Knight (1980) are actually the basisubcostale, a part of the basiradiale, the second axillary plate and the postmedian notal wing process, respectively.

The humeral plate and the unnamed plate of the Drosophilidae in Ferris (1965) are the basisubcostale and the basiradiale, respectively.

The basicosta of the Calyptratae in McAlpine (1981) is the basisubcostale.

The plesiomorphic condition and transformation of each structure is also discussed.

[translated from Japanese text in "Abstract of the 53th Annual Meeting of the Entomological Society of Japan": 35 (1993), the meeting held on April 3 –6, 1993]

Wing base structure of Diptera

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The interpretation of vein CuP in Diptera was simultaneously changed by Saigusa (1989) and Wooton and Ennos (1989) mainly based on the comparative morphology of wing venation between Diptera and Mecoptera. As a result of these works, vein CuP, vein A1 and anal cell in hitherto widely used terminology were interpreted as a thickened cuticular line (pseudovein), vein CuP and cell CuP, respectively. The new interpretation was supported by the comparative study of wing base structure between the two orders (Saigusa, 1993). However, the new interpretation is not widely used in current descriptive taxonomy. In this presentation I forward a plesiomorphic condition of the wing base in Diptera, propose a new terminology of detailed parts of wing base structure for the convenience of future comparative morphological work of the wing base, and criticize published works on the wing base of Culicidae (Harback & Knight, 1980), Drosophilidae (Ferris, 1965), and Calyptratae (McAlpine, 1981). The wing base structure of Diptera has the following characteristics: (1) the basicostale is reduced in size, and located below base of vein C, (2) the basisubcostale is distally enlarged forwards, where it is approximated to upper part of base of vein C, and its proximal end has loose articulation with anterior process of 1st axillary, (3) the vein Sc has a weakened membranous area on anteroventral part near its base, (4) the basiradiale is posteriorly separated from 2nd axillary by a narrow membranous slit, and its proximal end is closely articulated with basal part of anterior process of 1st axillary, (5) basal swelling of clavus is prominent, and the middle portion of its anterior margin is articulated with posterior margin of vein R stem, (6) a longitudinal internal ridge develops between veins A1 and A2, (7) the jugal area composed of bending cuticle lacks in any vein.

Keywords: comparative morphology, wing base, Diptera, CuP, anal cell

[Abstract of the oral presentation at the 6th International Congress of Dipterology, held in Fukuoka on 23-28 October, 2006]

Asio-Nearctic disjunct distribution in Diptera

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Although Asia and North America are separated by the Bering Strait, some groups of Diptera are distributed exclusively in both temperate Asia, particularly eastern Asia, and North America. This Asio-Nearctic disjunct distribution was first pointed out for flowering plants by Asa Gray (1860), and the origin of this distribution is mostly explained as a relict of the Arcto-Tertiary flora, which survived during the Pleistocene in glacier–free areas in eastern Asia and North America but destroyed in Europe. This distribution pattern was then detected in several groups of insects including Diptera and other arthropods (Esaki, 1932, Linsley, 1963, etc.). In this presentation, I list the groups of Diptera that show the Asio-Nearctic disjunct distribution, divide it into several subtypes according to their range, and also to taxonomic level. In Diptera at least the following groups show an Asio-Nearctic disjunct distribution (In some groups limit of range in Asia extends to N. W. Himalayas and the Altai; some have a few exceptional representatives in Europe): Tipulidae (*Cladura*), Trichoceridae (*Paracladura*), Tanyderidae (*Protoplasa*), Ptychopteridae (*Bittacomorphella*), Axymyiidae, Cramptonomyiidae Keroplatidae (*Robsonomyia*, *Fenderomyia*), Ditomyiidae (species gp. of *Symmerus*), Mycetophilidae (*Loicia*, *Aglaomyia*, *Acomoptera*, some gps. of *Boletina*), Blephariceridae (*Agathon*, *Philorus*, *Bibiocephala*), Deuterophlebiidae, Thaumaleidae (*Trichothaumalea*, *Androprosopa*), Chironomidae (*Chasmatonotus*), Rhagionidae (*Dialysis*, *Litoleptis*), Xylophagidae (*Glutops*), Dolichopodidae (*Diostracus*), Empididae (*Megagrapha*, *Euhybus*, *Hoplocyrtoma*, *Hesperempis*, *Trichoclinocera*, *Proclinopyga*, *Ochterohilara*, subgen. *Calorhamphomyia*, the *arakawae* gp. and *unbilicata* gp. of *Rhamphomyia*). The immature stages of most of these groups are either aquatic or sylvicolous, living in soil or rotten wood. The above list does not include any group of Brachycera (Muscomorpha). It is important to clarify in the future the origin of this distribution through detailed analyses of their phylogenetic relationships using both morphological and molecular characters – focusing particularly on the time of differentiation of the counterparts of the disjunct distribution.

Keywords: biogeography, Asio-Nearctic disjunct distribution, Arcto-Tertiary flora, Diptera

[Abstract of the oral presentation at the 6th International Congress of Dipterology, held in Fukuoka on 23-28 October, 2006]

Torrenticolous Empididae from northern Argentine Patagonia

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Through a recent field survey of torrenticolous empidids in northern Argentine Patagonia, eight species representing five genera, three known and two undescribed, were found. The monotypic genus *Dipsomyia* Bezzi is represented by an undescribed species that differs from the type species, *Dipsomyia spinifera* Collin known only from Chile, by yellow mesonotal bristles and more symmetrical fork of R4 and R5. Two males of *Proagomyia torrentium* Collin were found near its type locality. *Asymphyloptera* hitherto unknown from Patagonia is represented by an undescribed species that has a unique combination of four scutellars, incomplete fringe along posterior margin of basal area of wing and the presence of humeral crossvein, and belongs to neither the New World group nor the Australian group (Sinclair, 1995). An undescribed genus containing 4 moderately large undescribed species is similar to *Dipsomyia*, and has bare compound eyes, elongated, stout and recurved proboscis bearing setal brushes on apical portion of epipharynx, porrect maxillary palpi, setose laterotergites and broadly flattened 5th tarsomeres laterodistally produced into short processes. The genus appears to be a member of the *Ragas*-group (Sinclair, 1999), and it is extremely diversified in male genitalia, female terminalia and wing shape, vestiture and markings. They feed on small insects on wet stones in mountain brooks. The other undescribed genus somewhat similar to the former contains a small undescribed species characterized by flagellomeres incorporated into an elongate segment with tiny apical seta or style, drooping maxillary palpi and simple 5th tarsomeres.

Keywords: torrenticolous Empididae, *Ragas*-group, *Asymphyloptera*, *Dipsomyia*, Argentine Patagonia

[Abstract of the oral presentation at the 6th International Congress of Dipterology, held in Fukuoka on 23-28 October, 2006]