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PERMIAN FOSSIL INSECTS FROM TIKHIJE GORY

Order *Miomoptera*

By A. MARTYNOV

(Présenté par A. Borisiak, membre de l'Académie des Sciences, le 25 mai 1930)

FIRST PART

THE NEW FAM. *ATACTOPHLEBIIDAE* AND ITS RELATIONS

Introductory

Among fossil Insects I collected in 1928 on the shores of the Kama-river, at the village Tikhije Gory, are many remains of wings of the order *Miomoptera*. Some of these wings belong to the fam. *Palaeomantidae* HANDL. and were described by me in 1928, some — proved to represent new forms. A discovery at Tikhije Gory of the fam. *Lemmatophoridae* SELL., which was known only from the Kansas deposits, appears to be very interesting. Here belong two species, representing a new genus. One concretion proved to be filled with remains of wings of a rather large insect, which I have described yet in 1928¹ under the name *Atactophlebia termitoides* MART. This description was somewhat insufficient, as it was made but from a fragment of a wing. I considered, provisorily, this form as belonging to the order *Protorthoptera*, fam. *Homalophlebiidae* (?). An examination of the long series of new remains of wings of this insect, some of which are perfect, demonstrated to me that it belongs, indeed, not to *Protorthoptera*, but to the order *Miomoptera*. The wing-venation in this form is rich, but primitive, and in all essential features is similar to that in the fam. *Lemmatophoridae*.

¹ Permian Entomofauna of North-East Europe. Trav. Mus. Géol. Ac. Sc. URSS, t. IV, 1928, pp. 1—118 (19 Plates).

I consider now the gen. *Atactophlebia* MART. as representing a new family, closely allied to the fam. *Lemmatophoridae*.

Careful analysis of the wing-venation in *Palaeomantidae* convinced me that this family is also allied to *Lemmatophoridae*, but represents a group with strongly reduced wing-venation. Thus, the order *Miomoptera*, as a complex of allied families, appears to represent a natural complex.

Further comparison with other groups revealed the very interesting fact that there exists, in the wing-venation, an obvious similarity between *Megaloptera* (*Sialidae*, *Corydalidae*) and some groups of *Miomoptera*. This allows us to hold up the question on the relations and origin of the whole complex of *Euneoptera* MART. (= *Endopterygota* or *Holometabola*).

As to the nomenclature of wing-venation, I consider now that many facts corroborate the opinion that the pale concave vein behind Cu, which I have been naming up to the present as A_1 , represents, indeed, CuP (cubitus posterior). Consequently the veins A_2 and A_3 of my former denomination should be named as A_1 and A_2 .

April, 1930

Order MIOMOPTERA

Ordo *Miomoptera* MARTYNOV, Zool. Anzeiger, Bd. LXXII, 1927, H. 3/4, SS. 99—109, Fig. 1, 2; Trav. Mus. Géol. Acad. Sci. URSS, t. IV, 1928, pp. 65—86, pl. V, 3; VII, 2; XI, 2, 3, 4, 5; XIII, 1—6; XIV, 1, 2, 3, 4; XVI, 3.

Syn.: *Protombiaria* TILLYARD, Australian Insects, Sydney, 1926, p. 122.

+ *Protoperlaria* TILLYARD, Nature, London, 1926, pp. 828—830; Amer. Journ. Sci., vol. 16, pp. 185—220; vol. 16, 1928, pp. 313—348.

+ *Embiopsocida* TILLYARD, Amer. Journ. Sci., 16, 1928, pp. 469—484.

I consider it necessary to describe at first the new family *Atactophlebiidae*, which represents the most archaic group in the order. The problem of the relations of the order *Miomoptera* I will discuss later.

Fam. ATACTOPHLEBIIDAE, n. fam.

Anterior wings of more or less leathery consistency. SC long, though not reaching the apex of wings; RS also long, directed outwards, simple or with narrow main fork. M early dividing into convex and chitinised MA, bearing 2—3 branches, and twobranchied MP, anterior branch, MP_1 , being pale, unchitinized, concave, but bearing normal, that is, chitinized and dark apical branches, posterior one, MP_2 , of usual, normal aspect, chitinized and

dark, variously branched. CuA dividing near its base into three long branches, two outer branches constituting CuA₁, inner one — CuA₂; CuP straight, pale, concave. Anal region narrow, but high; A₁ and A₂ strong, the latter repeatedly branching. Cross-veins irregular, forming nearly a net. Secondary branches of M, Cu and RS very variable, often interchanging with their neighbours.

Venation of the posterior wings resembling that in the anterior ones, but their anal region is dilated into a fan. RS coalesced, at a short space, with MA₁. MP coalesced in a similar mode with CuA. CuP and A₁ long, A₂ forming, probably, several radial branches, supporting an anal fan; jugal region of it, probably, small.

Structure of the body, probably, in many features is similar to that in *Lemmatophoridae*, but the size is larger.

The family contains, at present, a single gen. *Atactophlebia* MART., from Upper Permian of Tikhije Gory.

Gen. *Atactophlebia* MART.

Gen. *Atactophlebia* MARTYNOV, Trav. Mus. Géol. Acad. Sci., URSS, IV, 1928, p. 51.

This genus was described by me but from a fragment of a wing. Moreover, a comparison with good series of wings in the present collection reveals some defaults in the homologisation of some veins in anterior wings, and thus, a new description of the genus appears to be necessary.

Description.

Anterior wings somewhat leathery, elongated. Costal area not large. SC long, ending with its weakened end-portion on the costal margin. RS deriving early from R and forming usually a long; narrow fork. M dividing somewhat earlier than R, MA forming 2—3 branches in its distal portion. MP₂ similar to MA, but dividing earlier; MP₁ — pale, concave, but with normal, dark end-branches. All secondary branches of M and of RS variable, not quite determinate. All three branches of CuA variously branching and often interchanging with each other by their branches. A₁ strong, but simple. A₂ branching. Cubito-anal region high; anal region much compressed. All longitudinal veins straight and the branches of RS, M and Cu, approximately, parallel. Cross-veins also varying, often bearing an aspect of an irregular net.

In the posterior wings Sc is a feeble vein, running near to R. RS similar to that in anterior wings, but its basal portion is coalesced with MA; MP_1 pale, vanishing to the apex of wings; MP_2 united at its base with CuA_1 . CuA_2 strong; basal portion of M coalesced at a short space with CuA_1 . Anal region dilated, supported, chiefly, by the branches of A_2 , arranged radially. The net much more sparce.

Wing-pads directed obliquely outwards and hindwards.

Atactophlebia termitoides MART.

(Figs. 1—10)

Atactophlebia termitoides MARTYNOV, Trav. Mus. Géol. Acad. Sci. URSS, vol. IV, 1928, pp. 51—52, pl. V, fig. 1; pl. IX, fig. 1.

Specimens in the collection № 2295 (Tikhije Gory; the end of VI, commencement of VII, 1928).

Concretion 66A. №№ 1—8 — complete or almost complete anterior wings; №№ 9, 10 — fragments of fore-wings; № 11 — hind-wing (fig. 5); №№ 12—14 — remains of wing-pads of nymphs.

Concretion 66B. Separate small pieces of shales with remains of wings. № 1 — anterior wing without anal region (fig. 2); № 2 — the whole anterior wing (fig. 1); №№ 3—5 — portions of anterior wings; № 6 — anterior wing without anal region (fig. 3); № 7 — distal half of an anterior wing; №№ 8—10 — fragments of wings; № 11 — basal portion of a fore-wing (fig. 4); № 12 — anterior wing (fig. 6); № 13 — hind-wing (positive) and the fragment of a fore-wing; № 14 — complete anterior wing (fig. 7).

Concretion 66C. № 1 — two fore-wings, placed one above the other; № 2 — fore-wing, damaged in its anterior portion; № 3 — anterior wing, without basal portion (reverse of № 14, concr. 66B); №№ 4—9 — parts and fragments of anterior wings?; №№ 10, 11 — anterior wings without basal portions; №№ 12, 13 — portion and fragments of an anterior wing; № 14 — basal portion of a posterior wing and two fragments of anterior wings.

Concretion 66D. №№ 1a, 1b — basal portion of anterior wing; №№ 30a, 30b — anterior wing, without anal portion; № 46 — anterior wing, not complete; №№ 47a, 47b — anterior wing (fig. 10); № 48 — portion of an anterior wing; №№ 54a, 54b — fragments of an anterior wing; № 63 — portion of an anterior wing.

Thus, there are about 18 remains of perfect, complete, or almost complete anterior wings, not less than 20 smaller portions or fragments of wings and 3 remains of posterior wings, but without anal region. Moreover on the concretion 66 exist several impressions of wing-pads (fig. 8 and 9) and of portions of tergites of nymphs.

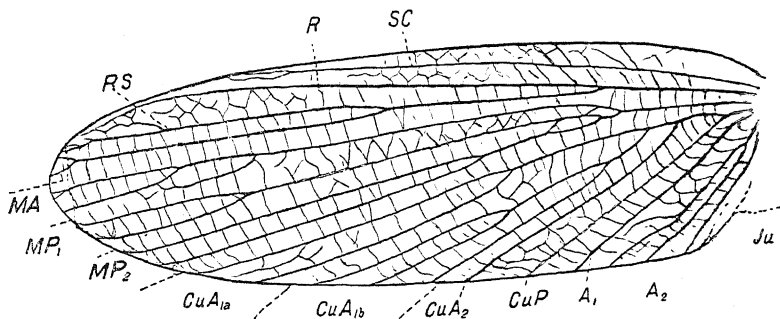


Fig. 1. Anterior wing of *Atactophlebia termitoides* MART. (Spec. 66B, 2a).

The concretion № 66 is found at the shores of Kama-river, just under the village of Tikhije Gory. Separate remains are found in different places, but also on the shores of Kama, near Tikhije Gory.

Description.

Anterior wings or tegmina elongated, narrowing to their apices, with convex costal margin. Elements of the net reveal a tendency to form

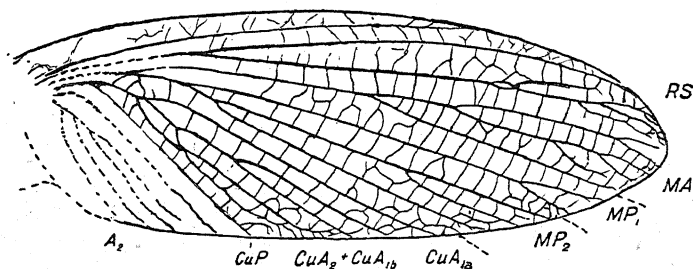


Fig. 2. Anterior wing of *Atactophlebia termitoides* MART. (Spec. 66B, 1).

rows of cross-veins, usually, irregular and partly anastomosing. SC ending on costa at 3/4 of the length of wing. Distal portion of R weakened and curved backwards to the apex. RS deriving from R at the base of the second fourth of wing, somewhat deviating from R and forming, usually, a narrow fork of variable length. Anterior branch of this fork not unfre-

quently forms, in its distal portion, several short irregular branches, directed obliquely forwards (figs. 3, 6).

M divides a little earlier than R; MA parallel to RS, with 2—4 branches of variable length; MP_1 with variable fork, MP_2 usually dividing.

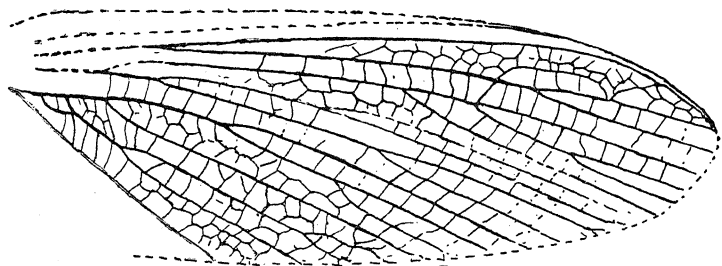


Fig. 3. Anterior wing of *Atactophlebia termitoides* MART. (Spec. 66B, 6).

into two long branches, anterior one sometimes furcating again. Branches of CuA_{1a} and CuA_{1b} , usually, long and subparallel. CuA_2 , sometimes also forming analogous branches, but in such a case CuA_{1b} is simple. CuP pale, straight;

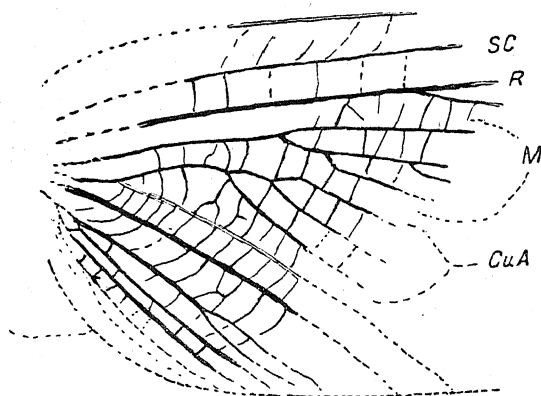


Fig. 4. Basal portion of a fore-wing of *Atactophlebia termitoides* MART. (Spec. 66B, 11).

A_1 strong, simple; A_2 also strong and forming a bundle of 3—4—5 branches, directed obliquely backwards (figs. 1—4, 10).

Posterior wings membranous, but the venation in the costo-cubital portion resembles rather closely to that in the anterior wings. MA united in its basal portion with RS and then forming as a branch of RS (fig. 5).

MP_2 united in its basal portion with CuA_{1a} and forming with it three longitudinal veins (in our specimen; number and relations of these

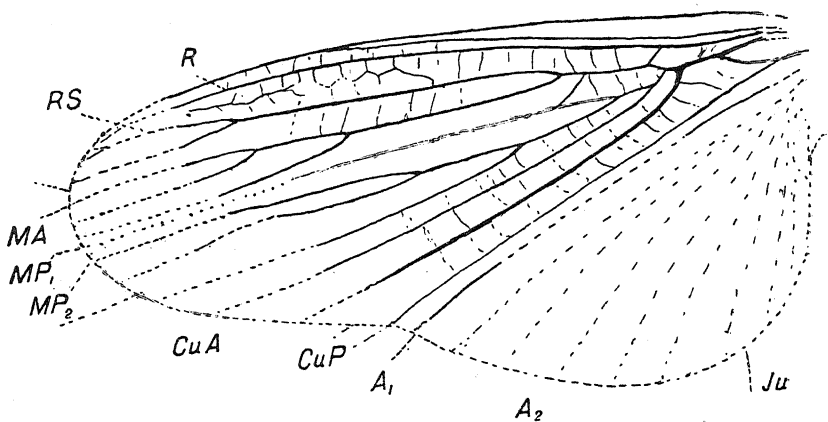


Fig. 5. Posterior wing of *Atactophlebia termitoides* MART. (Spec. Concr. 66A, 11).

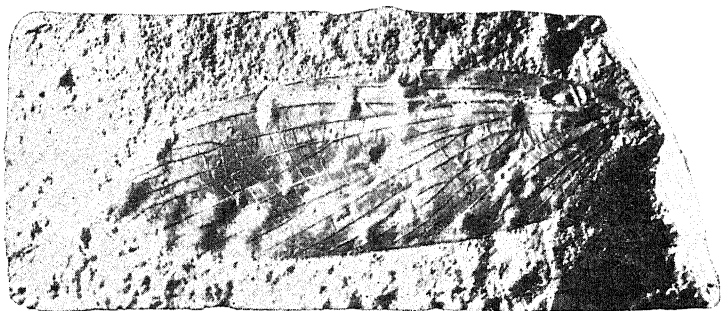


Fig. 6. Anterior wing of *Atactophlebia termitoides* MART. (Concr. 66B, 12; photograph).



Fig. 7. Anterior wing of *Atactophlebia termitoides* MART. (Concr. 66B, 14; photograph).

branches are, probably, considerably varied). CuA_1b simple, slender, CuA_2 simple, but strong. CuP slender. A_1 stronger; A_2 forming, probably, several radially arranged branches. The net is much more sparse and slender than in the anterior wings.

Length of anterior wings varying, 27—40 mm.

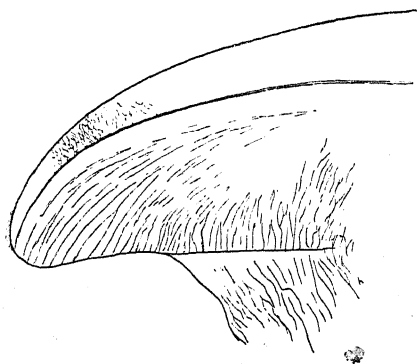


Fig. 8. Anterior wing-pad of *Atactophlebia termitoides* MART.

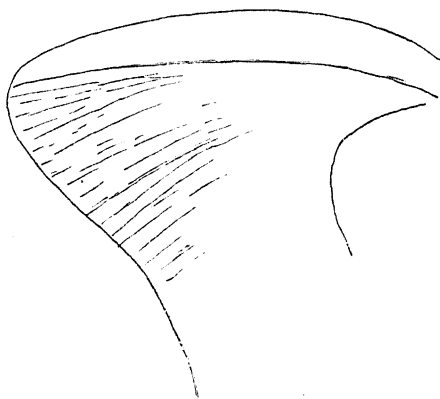


Fig. 9. Posterior wing-pad of *Atactophlebia termitoides* MART.

Shape of nymphal wing-pads (figs. 8 and 9) reminds much that in palaeozoic Blattoids (as they are figured by SELLARDS¹ and by HANDLIRSCH²) and in recent *Plecoptera*.

Variability.

The wing-venation in *A. termitoides* is of very variable nature, and one cannot find two wings with the same venation. This variability is, evidently, an individual variation of fluctuation, and one cannot to consider the types of these variations as some varieties. Such a variability reminds us of that in *Blattodea* and in *Gryllacridae*, proving that the separate veins here have not yet acquired quite determinate mechanical functions; therefrom their variations and frequent interchangings in some branches of M and Cu.

Length of fore-wings varies from 27 to 40 mm, and some of the variations in the venation are correlated with the difference of size.

¹ E. H. SELLARDS. Some new structural charaters of Palaeozoic Cocroaches. Amer. Journ. Sci., XV, 1903, Pl. VII. — A study of the structure of Palaeozoic Cocroaches. Am. Journ. Sci., XVIII, 1904, pp. 126, 128, 133.

² A. HANDLIRSCH. Die fossilen Insekten. Taf. XVII, XVIII.

For the typical form of the species I took the large form with more complete venation; example of such a form is represented in the fig. 1. Length of this wing is 40 *mm.* RS forms here a long, narrow fork; MA and MP_1 divide in their distal parts, MP_2 — in its basal part; branches of M do not coalesce with RS or with Cu.

Large wings have, usually, more or less determinate venation, but I sought few specimens with obvious distinctions or aberrations.

Variations of RS. The fork of RS may be shorter. The shortening and, finally, a complete reduction of this fork we meet with, mainly, in smaller specimens. In the specimen, which I described and figured in 1928¹

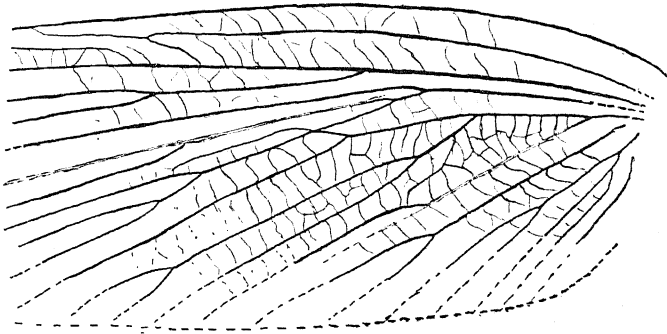


Fig. 10. Basal part of a fore-wing of *Atactophlebia termitoides* MART. (Spec. 47b).

we observe a simple RS, but with several irregular short branches anteriorly. Tendency to the complete reduction of the fork of RS is obvious in the small wing, represented in the figs. 2 and 6. In such cases we observe almost invariably several few short branches anteriorly, but RS never forms any distinct branches backwards (difference from *Protorthoptera* and from *Protoblattoidea*).

Variations of M. MA forms 2—3, sometimes, 4 branches, directed outwards; rarely they do not reach the end of wing. The stem of MP_1 is always pale, unchitinized, concave, but its apical branches are normal, that is, chitinized, dark and rather convex. Sometimes, hind dark branch originates nearer to the base. In one specimen (concr. 66C) pale MP_1 in its distal half suddenly becomes dark and convex.

¹ L. c., pl. X, fig. 1. The RS is named in this paper as R, MA as RS and R (damaged in its apical portion) as Sc.

Careful examination reveals that the pale portion of MP_1 , at the point of junction with the dark one, is bent forwards and soon vanishes. It is evident that the dark continuation is here the branch of MP_2 , which is detached from this vein and, finally, has supplanted the distal pale portion of MP_1 . In one specimen there is an interchanging in branches with MA. MA is here simple; MP arises as a dark convex vein, then divides into two branches, posterior one pale and anterior dark and normal. This last vein is, doubtless, the hind branch of MA, detached from MA and united to MP_1 . As a rule, M runs, in the basal part of wing, separately from Cu, but in the specimen № 14, concr. 66B (fig. 7) the stem of M is coalesced with the common stem of CuA, like as in the gen. *Sellardsia* TILL. or in the gen. *Lecorium*. SELL.

Variations of Cu. Branches of Cu are, usually, isolated from those of M, but sometimes MP_2 unites with the anterior branch of CuA_1a (fig. 10). Analogous union we meet with in the hind wing, represented in the fig. 5; besides, such an union or assimilation, in the hind-wings, of MP_2 with CuA_1a is, probably, more usual. In one specimen (concr. 66C) CuA_1a is completely adjoined to MP_2 and detached from CuA_1b . Thus, CuA became here but two-branched vein. CuA_1b and CuA_2 are also subject to various changes; compare, for instance, figs. 1, 2, 3, 10. CuP pale and simple, but some specimens exist, in which, as the specimen 47b (fig. 10), it divides into two branches, anterior one being dark and convex, posterior pale and soon disappearing; it is evident that the anterior dark vein represents the hind branch of CuA_2 , which is detached from this vein and adjoined to CuP, and, even, tends to supplant the distal continuation of true CuP.

A_1 is, usually, simple. Branching of A_2 varying, but the usual number of its branches is 3—5.

The net varying, being more sparse in smaller specimens.

Relationships of the family *Atactophlebiidae*

I will now examine the relations of this family. The most characteristic features of *Atactophlebiidae* are the structure of R, RS, M, the structure and configuration of Cu and of the anal region, behaviour of these veins in the posterior wings and, finally, the strong variability of the whole wing-venation. These characters, although somewhat modified, we meet with also in the fam. *Lemmatophoridae*, therefore the fam. *Atactophlebiidae* should be

included, together with this family, in the same order *Miomoptera*. On the other side, *Atactophlebiidae* in many characters of their wing-venation show rather obvious resemblance to the orders *Blattodea*, *Mantodea* and, even, to *Isoptera*. Thus, by the fam. *Atactophlebiidae* the whole order *Miomoptera* proves to be allied to the order *Blattodea*, especially, to more archaic groups of it. Let us to consider different parts of wing-venation separately.

Relations to *Blattodea*.

System of R. The conformation of RS, directed rightly outwards and forming but few (1—3) narrow forks in its distal part, differs strongly from that in *Orthoptera* (*Protorthoptera*), in which RS forms usually a row of oblique branches hindwards. It is true that these branches are absent in such forms, as *Palaeocixius*, *Fabrecia*, *Prototettyx*, *Camptoneurites*,¹ but these genera are aberrant among *Protorthoptera* and stand more or less near to *Paraplecoptera* (*Spanioderidae* and allied genera), and to *Plecoptera*, which, in some features, manifest their affinity to *Blattodea* (s. l.). RS and R in the wings of *Atactophlebia* remind, indeed, very much the same veins in the hind wings in many *Blattodea*, for instance, in *Blaberidae*, *Polyphagidae*, *Periplanetidae*, as well as in some fossil forms. Radial complex in the tegmina of *Blattodea* and of more archaic *Isoptera* (fam. *Mastotermitidae*) is not yet differentiated into R and RS and forms the series, sometimes abundant, of branches, running obliquely forwards and outwards. Such a structure of R is not yet mechanized, that is, adapted to some definite mechanical functions in the flight, but leathery tegmina of *Blattodea* are not yet transformed in the membraneous wings. They are not more than the enlarged and separated (by the membraneous articulation) paranotal processes, which acquired a net of vein-shaped blood sinuses. Analogous condition one may observe also in the prothoracal lateral expansions in some *Blattodea*, for instance, in *Blaberidae*. Analogous structures have had, probably, prothoracal alulae in *Palaeodictyoptera*, then in *Lemmatophoridae*, among *Miomoptera*. Because the tegmina of *Blattodea*, — except such forms as *Polyphagidae* and few others, — as a rule, do not function as organs of flight, their tegmina-venation remains unmechanized, in other words,

¹ I would propose the new name *Camptoneurites*, nom. nov., to the gen. *Camptoneura* MART. (Trav. Mus. Géol. Ac. Sci. URSS, 1928, p. 53), the last name being a nomen praeoccupatum. The family one should name the fam. *Camptoneuritidae*, n. nov.

retains its very archaic condition. Posterior wings had once a similar, tegminal structure and shape, and similar tegmina-venation, because both pairs of «wings» are developed, doubtless, from the two homonomous pairs of paranotal expansions. Later on, metathoracal tegmina started gradually to adapt themselves to the flight, which was, at first, a sort of soaring or gliding, and in connection with such a function began some dilatation of the hind tegmina, in their cubitoanal portion, especially. As a result of this dilatation became certain dechitinization, or «membranization» of these tegmina, that is, their transformation in the wings. This «membranization» resulted, at first, in the anal portion, which developed into an anal fan. In accordance with the new function the venation began also to modify, adopting gradually an arrangement more comfortable to the mechanical requests of the flight. Structure of veins is also modified: main veins became more chitinized, more tough. Anterior (costo-radial) portion in the hind wings was often subject to an abbreviation or compression, consequently, SC, as well as the primitive radial complex, inevitably started to reduce their (anterior) branches. In this process, as a rule, middle branches disappeared, strong basal branch and a variable number of distal branches of R were retained. This strong basal branch is that vein, which we name R, the remaining portion RS (figs. 11 and 12). This process one can examine in *Blaberidae*, *Polyphagidae*, *Periplanetidae*, and in some others groups. Certainly, it did not proceed uniformly, but in rather variable ways.

The apical portion of RS invariably bears a series of short branches, directed obliquely forwards. A comparison with the wings in *Atactophlebia* reveals an obvious similarity in the conformation of RS and R in both these groups. As we mentioned above, anterior distal branch of RS in *Atactophlebia* forms, sometimes, several short branches, directed forwards and, usually, irregular. They represent last remains of anterior branches of the former primitive radial complex.

Thus, the structure of RS in *Atactophlebiidae* (and also in *Lemmatophoridae*) resembles to that in *Blattodea* and differs much from that in most *Orthoptera*. Oblique hind branches of RS of *Orthoptera* did not yet developed in our family, as also in most *Blattodea*;¹ this condition of RS is, thus, very archaic.

¹ The fam. *Polyphagidae* represents an exception from the general rule. In their wings from the distal portion of RS departs a whole series of branches, directed obliquely backwards.

Certain resemblance of the wings in *Atactophlebiidae* to those in *Isoptera*, especially in the fam. *Mastotermitidae*, is not surprising, as *Isoptera* are closely related to *Blattodea*.

In *Artinska* SELL. and in the remaining *Lemmatophoridae* R and RS are structured on the same plane, although this plane is not always quite distinct, as these veins, as well as the whole wing-venation in *Lemmatophoridae*, were subject of gradual reduction.

System of M. One of the most interesting characters in the wings of *Atactophlebiidae* is the dechitinized, pale condition of MP_1 , whereas MA and MP_2 are of the normal structure, dark, chitinized and rather convex. Such a conformation of M, apparently, is quite lacking in true *Orthoptera*, but we meet with similar structure in the fam. *Lemmatophoridae* on the one side, and in the fam. *Sialidae* (order *Megaloptera*), on the other side.

Moreover, an obvious similarity to the condition of M in *Atactophlebiidae* we meet with also in the hind-wings of *Blattodea*, especially in the fam. *Periplanetidae*, *Polyphagidae*, *Blaberidae*. In the tegmina of *Blattodea* M forms, sometimes at once, several branches, enough homonomous and variable, or divides early into two main branches, furcating again, but here an alternation of convexities and concavities is yet lacking.

In the posterior wings the M-complex was subject to rather great modifications. Costo-cubital portion in the hind wings in *Blattodea* retains, mostly, a somewhat leathery consistency, and the needs of some bending in flight and in the folding the wings, when at rest, conditioned the formation of a longitudinal stripe of very thin and pale chitin just behind the M. Similar stripe or «anal furrow», along CuP, is formed in the anterior wings in *Blattodea* everywhere; in the posterior wings this «anal furrow»

However, many details of their conformation prove that such branches in these *Blattodea* are not of primary, but, probably, of secondary nature, and that before, in their ancestors, R + RS had an usual «blattoid» structure. These hind branches of RS are formed, probably, by a sort of reconstruction or «recrystallization» of some apical branches of R + RS and of M, partly of some elements of the primitive net. Such a reconstruction proceeded in the connection with dechitinization (membranization) of the distal parts of tegmina (in both anterior and posterior pairs) and with adaptation of them to the flight. It appears to me very probable that the series of oblique hind branches of RS not only in *Orthoptera* (+ *Protorthoptera*), but also in *Protoblattoidea* and in some *Palaeodictyoptera* developed also secondarily, by an analogous process of reconstruction (here, chiefly, of the primitive net), as a reaction to the mechanical requests of the flight. The wings in *Orthoptera*, «*Protoblattoidea*», *Palaeodictyoptera* and, partly, in the remaining insects overpassed formerly some phases of structures, reminding of the tegmina of *Blattodea*. However, this does not signify that all groups of Insects developed from *Blattodea*.

is modified and became rectilinear. The median stripe of thin chitin usurped in most *Blattodea* the hind portion of M, which became also thin, pale, unchitinized and concave. On the contrary, anterior portion of M preserves, usually, its normal structure, that is, is dark and chitinized. Posterior pale portion of M, which sometimes completely vanishes, we may consider as MP, anterior, «normal» portion — as MA. Such a condition one may observe in *Petasodes*, *Polyphaga*, *Periplanetidae* and in some others. Whilst the stem of MP is pale and thin, its distal branches in these *Blattodea* prove

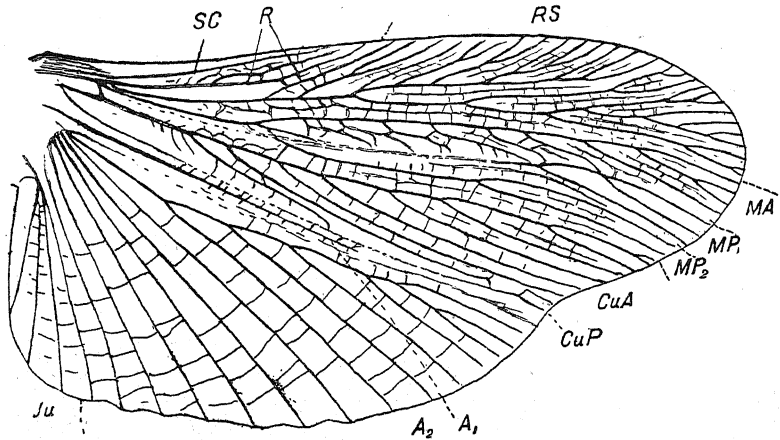


Fig. 11. Hind-wing of *Pseudoderopeltis compressipennis* ADEL. (for lettering see the text).

to retain, usually, the normal (dark) structure, as they do in *Atactophlebiidae* and *Lemmatophoridae*. Not infrequently, for instance in *Polyphagidae* and *Panchloridae*, MA unites,¹ for a short length, with RS, then separates, like as in *Atactophlebiidae* or in *Lemmatophoridae*. The condition in *Atactophlebia* differs in that MP is provided with a distinct hind branch of normal structure, that is, with MP₂. Therefore, the pale stripe is formed here not behind, but within the region of M (intramedian stripe). This distinction is not, however, absolute, as MP₂ sometimes, although rarely, occurs among *Blattodea*. I observed such a structure of M, for instance, in one specimen of *Pseudoderopeltis compressipennis* ADEL. (fam. *Periplanetidae*). One may perceive here (fig. 11) MA, pale, thin and vanishing to the base MP₁, and dark and chitinized MP₂.

¹ In the blattoid tegmina basal portion of M sometimes is placed very close and, even, also coalesces with R.

Thus, the composition of M in both *Atactophlebiidae* and *Lemmatophoridae* does not differ essentially from that in *Blattodea*. Analogous composition of M existed once, apparently, in the ancestors of *Plecoptera* (see below), but the present condition of M in the recent *Perlidae* is very different. In the hind wings of *Atactophlebia* MP_2 is united (in our specimen) with CuA_{1a} , without representing a separate branch of M.

System of Cu. CuA divides in *Atactophlebiidae* into three main branches (CuA_{1a} , CuA_{1b} , CuA_2) very early, near its base. CuP — straight, unchitinized, pale; it is placed here in cubital stripe («anal furrow»). The structure of Cu in *Orthopteroidea* is diverse enough, but mostly very different from that in *Atactophlebiidae*. A similar structure of Cu we meet with again

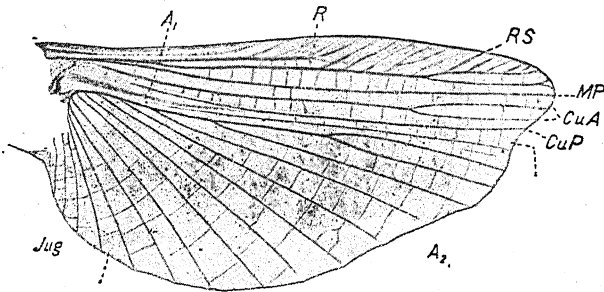


Fig. 12. Hind-wing of *Phyllodromia germanica* (for lettering see the text).

among *Blattodea*. In the blattoid tegmina CuA divides also early and forms branches of various numbers, usually, more than three. These branches may fork repeatedly. However, proximal branches of CuA manifest a clear tendency to some weakening and, finally, to complete disappearing, and not infrequently one may meet with the condition that CuA forms but three main branches, quite like as in *Atactophlebiidae*. Such a similar condition one may observe, for instance, in *Petasodes* (*Blaberidae*), *Shelfordella* (*Periplanetidae*), in certain *Epilampridae*. Three-branched condition of Cu in these *Blattodea*, besides, is in no way constant, but varies considerably. In the posterior wings of *Blattodea* this conformation of CuA does not reappear, and CuA represents here a strong stem, forming, behind, a series of branches, shortening to the base of CuA . In specialized forms (fig. 12) CuA loses the most of its branches. On the contrary, in the hind-wings of *Atactophlebiidae* CuA adopted, essentially, the same structure as in the forewings, but CuA_{1b} and CuA_2 are simplified. Thus, the structure of CuA in

Atactophlebiidae, though much resembling to that in *Blattodea*, is more specialized and more determinated than in this order. A very similar structure of Cu, but still more specialized and simplified, we meet with in the fam. *Lemmatophoridae*. The unlikeness of the conformation of Cu in anterior and posterior wings in *Blattodea* is correlated with the different shape and structure of anal region in both pairs of «wings». In *Atactophlebiidae* CuP is straight in both anterior and posterior wings, and it is comprehensible that CuA is formed in both in a similar manner. In *Blattodea* it is strongly curved in the anterior, straight in the posterior wings.

Anal region in the anterior wings of *Atactophlebiidae* is much different from that in *Blattodea*, being much narrowed, therefore A_2 , though ramified, is directed with its branches not outwards, to CuP, but obliquely backwards. By its general shape and by the conformation of A_1 and A_2 it much reminds of that in *Camptoneurites* MART. and in allied forms.

The structure of anal region in *Lemmatophoridae* is completely similar, but the branches of A_2 are, mostly, reduced or, even, lacking. The conformation of anal fan in the hind-wings of *Atactophlebiidae* was, doubtless, very similar to that in the gen. *Artinska*, for instance, but the venation in the first named family was, probably, more composite, therefore, more reminding that in *Blattodea*.

System of cross-veins or the net. In *Atactophlebiidae* the net is represented, chiefly, by rows of cross-veins, somewhat irregular. In wings of *Blattodea* the net is often represented also but by rows of cross-veins, but many genera exist, in which the primitive net is well preserved, at least, in the tegmina. In the palaeozoic cocroaches almost invariably existed a typical archaic net with numerous small cells. It is obvious that the evolution of the net proceeded in the direction from the condition in palaeozoic cocroaches to that in more specialized *Miomoptera*.

Prothoracal expansions. In the gen. *Lemmatophora* pronotum possessed, according to TILLYARD, two lateral rounded expansions, each with peculiar net of feeble «veins». Very similar system of radial, branching nervures we meet with in the prothoracal expansions in some *Blattodea*, for instance, in *Petasodes*, and in many palaeozoic forms. Such expansions in *Lemmatophoridae* differ, apparently, only in that they did not cover the head, which was free. It appears very probable that in *Atactophlebiidae* existed analogous prothoracal expansions.

Wing-pads. Nymphal wing-pads in *Atactophlebiidae*, as we have mentioned above, were very similar to those in *Blattodea*, in *Plecoptera* and in *Isoptera*.

Relations to *Mantodea*.

Wings of *Atactophlebiidae* and *Lemmatophoridae* in many characters remind also of *Mantodea*, which are closely related to *Blattodea*, but differ in their wing-venation being more mechanized and simplified. In the wings of *Mantodea* the stem of M is simple and concave, that is, represents MP; distinct MA is here lacking. In the posterior wings RS is long and derives from R, usually, near to the point of deviation from it of M, like as in *Blattodea*, but sometimes coalesces, for a space, with R. In the fore-wings such a long RS is absent, but R forms, usually, one branch in its distal part. One name this branch RS, but it is obvious that this RS is not quite homologous to RS in the hind-wings.

Conformation of CuA in *Mantodea* is more similar to that in *Atactophlebiidae*, and in the fore-wings this vein is, usually, composed of two main branches as in *Atactophlebiidae*. Anal region is somewhat simplified, but its structure remains yet different enough from that in *Atactophlebiidae* and *Lemmatophoridae*; it is not compressed and CuP is yet arcuate, as in *Blattodea*. In the character of net fore-wings of *Mantodea* resemble much to those of *Atactophlebiidae*.

Several genera of *Mantodea*, for instance, *Rhombodera* BURM., also possess broad prothoracal lateral expansions, somewhat reminding those in *Blattodea*, but differing in that the head remains free, not covered by any anterior expansion. These prothoracal expansions in *Mantodea*, doubtless, resemble those in *Lemmatophoridae*, but are not as projected and do not possess any venation. In the archaic *Blattodea*, on the contrary, such a venation persists. Thus, the presence of prothoracal expansions in *Lemmatophoridae* is not very extraordinary; in this character they remind of *Blattodea* + *Mantodea*.

Wings in *Isoptera*, especially in more archaic genera, as *Mastotermes*, resemble superficially to the wings in *Atactophlebiidae* (therefrom I named, in 1928, the species from Tikhije Gory *A. termitoides*), but differ from them more strongly than from those in *Blattodea*. Anal region of *Isoptera* is much reduced, but the character of reduction is different from that in

Miomoptera; anal region is here not compressed, but reduced, as the whole; CuP in *Mastotermes* remains arcuate.

The most *Protorthoptera* are far enough from *Atactophlebiidae* and *Lemmatophoridae*. Nearer to them stand the families *Lepiidae* SELL., *Idelidae* ZAL. and *Camptoneuritidae* MART., with their allies, but all they represent some aberrant side-groups of *Protorthoptera* and, perhaps, should be excluded from this order. In every case, they are more related to above named two families of *Miomoptera*, as well as to *Blattodea* + *Protoblattoidea*.

Lepiidae and *Idelidae*, doubtless, are rather closely related to *Atactophlebiidae* and represent remains of a group, from which also true *Miomoptera* developed. The separation of these branches took place, probably, already in the Upper-Carboniferous.

Relations to *Lemmatophoridae*.

We have already considered above these relations. For the elucidation of these interrelations one should turn, first of all, to more primitive forms of *Lemmatophoridae*, preserving the most complete venation. Such forms are represented by the gen. *Artinska* SELL., and comparison of its wings with those in *Atactophlebia* shows clearly that their venation is structured on the same plane (fig. 13), but in *Artinska* it is more simplified or mechanized. The consistency of the fore-wings in *Artinska* was, probably, more membranous.

Distal branches of M and Cu are, mostly, lacking in *Artinska*; the net is also much reduced, being represented but by sparse cross-veins. R and RS have similar aspect and the same relations. M is also similar, but MP₂ is lacking in *Artinska*, as well as in *Lemmatophoridae*, in general. Besides, the hind branch of MP₂ in the hind-wings of *A. clara* SELL. (fig. 13) is long and, apparently, has a normal aspect, therefore it represents, perhaps, MP₂.

CuA of *Lemmatophoridae* differs only in that the point of furcation of CuA₁ migrated somewhat backwards, consequently, the branches CuA_{1a} and CuA_{1b} became shorter. In the posterior wings CuA became already two-, not threebranched.

Anal region is also very similar, but the branching of A₂ is much more scarce; sometimes A₂ is simple. The variability of wings-venation in *Lemmatophoridae* also reminds of *Blattodea* and of *Isoptera*.

The fork of RS, existing in *Artinska*, *Sellardsia* and *Kazanella* n. gen., is lacking in *Paraprisca* HANDL., *Lecorium* SELL., and *Lemmatophora*. In the last named genus the venation is still more reduced, and only few cross-veins are retained; the main forkings of M and R migrated somewhat to the middle of wings; SC somewhat shortened. In the anal fan the number of branches of A₂ is three, the most proximal vein representing the jugal vein (*v. arcuata*).

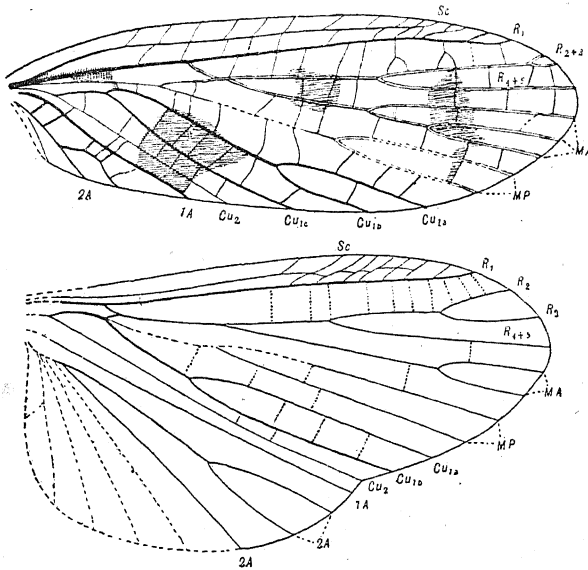
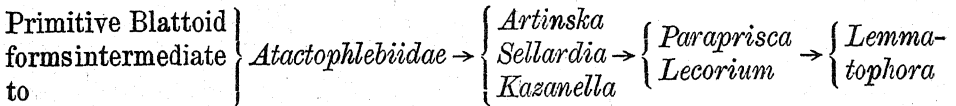


Fig. 13. Anterior and posterior wings of *Artinska clara* SELL (from TILLYARD, 1928 № 94, pp. 324, 328).

These modifications, resp. simplifications of the wing-venation from *Atactophlebiidae* to the most reduced types in *Lemmatophoridae* allow us to set out the following morphological row:



This is not a genetical, but only morphological row. It manifests that the type of wing-venation in *Lemmatophora* is formed by the intermediate conditions, in *Artinska* and *Atactophlebiidae* from that of some primitive unknown Blattoid ancestors. It does not represent the phylogenetic row.

Relations of *Plecoptera*

As I argued in the paper of 1928, the wing-venation in *Plecoptera* resembles partly to that in *Paraplecoptera*, partly to that in *Camptonewritidae* and allied forms. The structure of the body and of the appendages (genital and anal appendages) in *Plecoptera* reminds also of *Orthoptera* (*Acridodea*), although not closely. Some other structures in *Plecoptera*, for instance, composition of anal fan, in the posterior wings, resemble more to those in *Blattodea*. Anal fan in true *Orthoptera* differs from that in *Blattodea*, chiefly, in that the portion, supported by true anal veins (anal portion), is, comparatively, small, narrow, whilst the portion (jugal portion), strengthened by the jugal veins, is, comparatively, large. In *Blattodea*, as well as in allied *Mantodea* and *Mastotermitidae* (*Isoptera*), on the contrary, jugal portion is small, anal one — large.¹ In *Plecoptera*, as well as in *Miomoptera*, the anal portion of anal fan is also much larger than the jugal one, like as in *Blattodea*.

Relations to *Atactophlebiidae* and *Lemmatophoridae* are enough evident in many cases, but they are not very close. TILLYARD emitted newly (1926, 1928) a different opinion, according to which *Plecoptera* represent direct offshoots of the fam. *Lemmatophoridae*, namely of the gen. *Artinska* SELL.: «we may, I think, with considerable certainty, indicate *Artinska* as the actual ancestor of the existing order (i. e. *Plecoptera*)».²

Let us now compare the wing-venation in *Plecoptera* with that in *Atactophlebiidae* and *Lemmatophoridae* more thoroughly. Certainly, in this comparison one should keep in mind, chiefly, more primitive forms, which possess a most complete venation. Such forms are represented, chiefly, in the fam. *Perlodidae*, *Perlidae* and, especially, in the fam. *Pteronarcyidae*. Comparison of the wings in *Pteronarcys* NEWM., for instance, in *Pt. reticulata* BURM. (fig. 14) with those in *Artinska* and in other known *Lemmatophoridae*, reveals that the venation in *Pteronarcyidae* is much more complete than in *Lemmatophoridae*, therefore *Artinska* or, even, the family *Lemmatophoridae*, cannot be considered as representing the ancestors of

¹ This difference, as well as the whole problem of the interrelations of anal and jugal parts in wings is more thoroughly discussed by me in the article «Ueber zwei Grundtypen der Flügel bei den Insekten und ihre Evolution». Ztschr. f. Morph. u. Oekol. d. Tiere, Bd. 4, H. 3, 1925.

² Amer. Journ. Sci., № 94, p. 347.

Plecoptera. Comparison with the more primitive wing-venation in *Atactophlebiidae* also reveals some essential difference.

System of Cu. According to the general interpretation, both main branches of Cu in the wings of *Plecoptera* are CuA and CuP (the most authors name the vein CuP as Cu₂. However, this presumed CuP is not

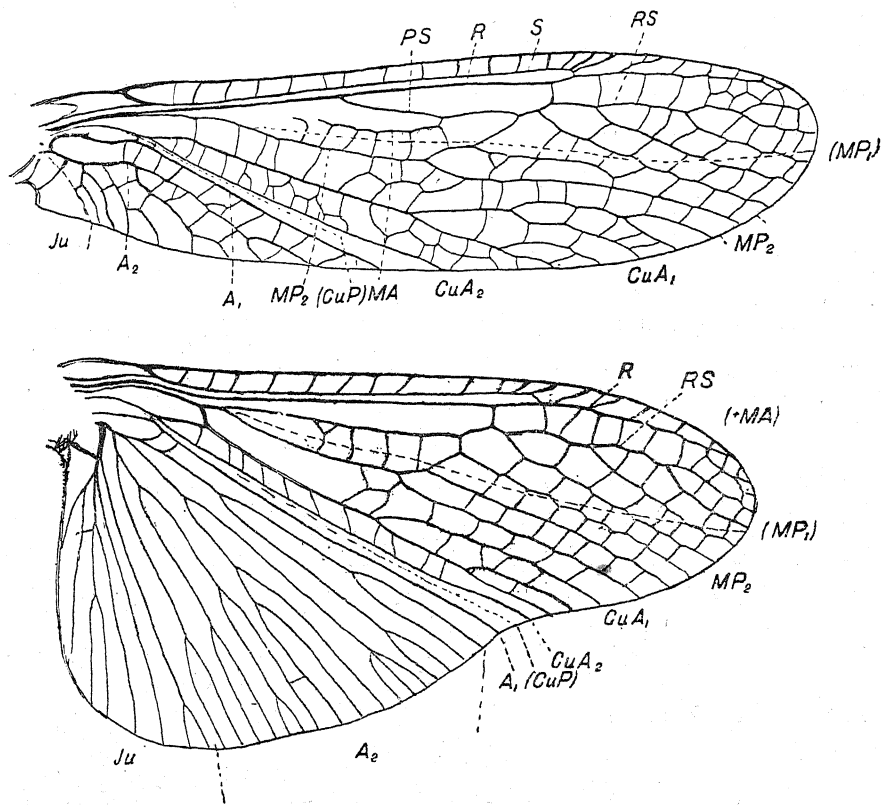


Fig. 14. Wings of *Pteronarcys reticulata* BURM.

pale, but dark and chitinized, and the whole forking of Cu reminds more of the forking of CuA in *Lemmatophoridae* than the main division of Cu into CuA and CuP. This allows to surmise that the hind branch of Cu, perhaps, does not represent true CuP. Further examination reveals that just behind of the basal portion of this vein exists a very concave stripe, prolonging then in the more shallow concavity between this vein and A₁. It becomes evident that this stripe is homologous to the similar stripe along CuP in *Atactophlebiidae* or to the «anal furrow» in *Blattodea*, but the corresponding vein,

namely true CuP, of this stripe is reduced and completely disappeared. Thus, the posterior main branch of Cu is not CuP, but CuA₂, anterior one — CuA₁. Being placed close to the stripe, CuA₂ appears as a concave vein, but primarily it was not concave. According to this interpretation Cu, or, more correctly, CuA in the fore-wings of *Plecoptera* proves to resemble to that in most *Miomoptera*. In the hind-wings of *Plecoptera* CuA does not enter into an union or coalescence with M (distinction from *Miomoptera*). The vanishing of CuP in both pairs of wings in stone-flies is caused, doubtless, by the strong «membranization» of wings, and by the narrowing of the area between CuA₂ and A₁.

System of M. M in the wings of *Plecoptera* appears as being simple, though forking in its distal half, but as I showed in my previous article,¹ it is actually composed of two main branches, MP (=M of authors) and MA. On the base of the obvious similarity in the configuration of M and RS between many *Plecoptera* and the gen. *Camptoneurites*, I came to the conclusion, that MA in stone-flies is united with RS, more or less like as in that genus. Then, in the anterior wings the basal portion of MA, in the posterior ones the basal portion of RS, are reduced and vanished in *Plecoptera*. TILLYARD emitted a different opinion,² according to which M in the wings of *Perlaria* is MA, MP being lacking. He based, chiefly, on the fact, that M of *Perlaria* is a convex vein. However, in the interpretation of veins in orthopteroid insects — and *Plecoptera* may be considered as belonging to this complex — it is difficult to base only on the convexities and concavities, as in these insects some main vein not infrequently adopte an unusual position. I will call to mind that in fore-wings of *Locustodea*, for instance, CuA is concave, M and MP convex. In *Acridodea* CuA also appears to be rather somewhat concave.

Examination of the region of M in *Pteronarcys* demonstrates that MA exists also in the fore-wings, but does not reach the stem of M. In our specimen (fig. 14) it is placed behind the stem of RS and is connected with MP by five cross-veins. In the posterior wings it is connected with MP in a quite similar mode; there are but three such cross-veins, but the basal one is forked and, consequently, probably composed of two veins. Examined

¹ Permian Entomofauna of North-East Europe. Trav. Mus. Géol. Ac. Sc. URSS, t. IV, 1928, pp. 55, 56.

² Amer. Journ. Sci., 1928, № 94, pp. 208, 209.

portion of MA exists in all specimens of *Pt. reticulata*, but varies; besides, the mode of variation (the number of cross-veins, their disposition) is very similar in both pairs of wings. In the anterior wing in a specimen of *Megar-cys ochracea* KLP. (var. n.) from the fam. *Perlodidae*, one may perceive even the basal portion of MA (fig. 15), although not connected with RS.

All these facts prove clearly that true MA is existing in *Plecoptera*, but is adjoined to RS. Its distal continuation is not always distinct. In posterior wings the basal portion of RS vanished, and thus, MA usurped the whole RS. Analogous condition one may meet with in some *Orthoptera*.

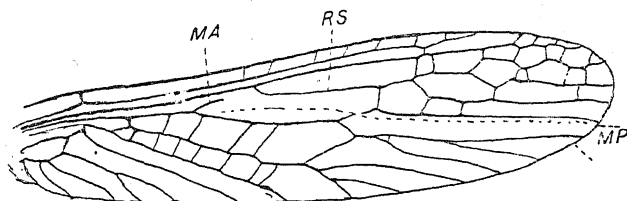


Fig. 15. Anterior wing of *Megar-cys ochracea* KLP.

Now, what is, morphologically, the hind branch of M, or MP, in *Plecoptera*? Does it represent an unique, undivided MP (although with two distal branches), or is it MP_2 , or MP_1 ?

In both anterior and posterior wings in *Pteronarcys* NEWM. (fig 14) one may easily perceive a longitudinal pale and very thin stripe, which is placed somewhat anteriorly from MP. This stripe is almost straight, crossing several cross-veins, as well as oblique hind branches (apparent!) of RS. It commences on MP, at the level before the origin of RS. In the posterior wings the stripe originates in the same point, just beyond the point of uniting of MA with MP. A similar stripe exists also in the wings of *Perlodidae* (fig. 15); it begins at the corresponding place. In *Perlidae* the stripe is somewhat indistinct; it is indistinct also in the fam. *Nemuridae*. Position of this stripe within the media and its union, at its base, with MP are quite the same as in *Atactophlebia*, and remind also of some *Blattodea*. At the bottom of this stripe is placed in *Atactophlebiidae* the pale and unchitinized MP_1 ; at the bottom of the similar pale stripe in *Blattodea* the corresponding vein is not infrequently completely obliterated. A very similar condition we meet with in *Pteronarcys* and in *Perlodidae*:

the stripe is retained, but the vein at its bottom, that is MP_1 , is already quite lacking. Thus, M in the wings of *Plecoptera* has had once a structure similar to that in *Atactophlebiidae*; it was composed of usual dark MA, of pale, unchitinized and concave MP , which afterwards was obliterated, and of usual dark and rather convex MP_2 . This MP_2 forms now the M of authors; it is twobranchied (MP_{2a} and MP_{2b}). The presence of the remains of the median and cubital stripes proves that the wings of the very remote ancestors of *Plecoptera* were once more leathery or tough; this is a conclusion to which we came earlier, when discussing the problem of the origin of these stripes or furrows.

The subsequent modifications of M in *Plecoptera* were as follow. MA is united with RS in both anterior and posterior wings. Then, the basal portion of MA in anterior wings is obliterated almost everywhere; similar condition we meet with in the fam. *Palaeomantidae*, among *Miomoptera* (see below). In the posterior wings, on the contrary, it is the base of RS, which vanished. An uniting of MA with RS exists also in the hind-wings, apparently, of all *Miomoptera*, but we should not forget that the similar union exists also in many true *Orthoptera*, for instance in *Locustodea*.

The basal portion of M in *Plecoptera* never coalesces with CuA, whereas in the hind-wings of *Miomoptera* such a coalescence exists everywhere.

System of R. Taking into consideration that MA is united with RS, we may conclude that RS in *Plecoptera* had primarily a structure, reminding that in *Atactophlebiidae* or, even, in *Lemmatophoridae*. It was directed outwards and had but few, 1—2, branches, directed also outwards. Such a condition we meet with in *Perlodidae* (fig. 15) and in other families, except *Pteronarcyidae*. In *Pteronarcys* from the stem of RS derive several branches, directed obliquely hindwards and crossed by the pale median stripe. However these oblique branches of RS in *Pteronarcys* are, doubtless, of secondary nature. Earlier, in the ancestors of *Pteronarcys*, RS has had, certainly, an usual structure, analogous, for instance, to that in *Perlodidae*, and the median stripe, which is an archaic structure, inherited from the leathery stade of ancestors of *Plecoptera*, was placed, certainly, behind $RS + MA$. Consequently, oblique branches under discussion are secondary and developed later on, by a sort of reconstruction of the original branches of RS, of MA, as well as of intermediate cross-veins. Such an origin of these branches reinforce our hypothesis of a similar origin of oblique

branches of RS in «*Protoblattoidea*» (they are rather «*Para*»- than «*Proto*»-*blattoidea*) and in *Orthoptera*.

Anal region is longer than in *Miomoptera*, A_2 is not compressed as in *Atactophlebia*, but rather broadened. Ano-jugal fan resembles to that in *Lemmatophoridae*.

The facts and considerations, just exposed, prove that *Plecoptera* are, indeed, related to *Miomoptera*, to *Atactophlebiidae* especially, but one cannot derive them from both *Atactophlebiidae* and *Lemmatophoridae*. The wing-venation in *Lemmatophoridae* — and still more in *Palaeomantidae* — is too reduced, more than in many families of *Plecoptera*. *Atactophlebiidae* are more archaic, but they adopted a somewhat different path of evolution than that of *Plecoptera* and, doubtless, are completely extinct, like to *Lemmatophoridae*. Thus, *Plecoptera* may be considered but as a side branch of *Miomoptera*, although developed, probably, from some common roots with *Miomoptera*. They are not extinct, perhaps, thanks to their aquatic mode of life.
