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ON SOME NEW REMARKABLE *ODONATA* FROM THE PERMIAN OF ARCHANGELSK DISTRICT

By A. MARTYNOV

(Présenté par A. Borisiak, *membre de l'Académie des Sciences)*

In 1923 I expressed the opinion[1] «that in the shape of wings, as well as in the general disposition of the main longitudinal veins and in smaller reduction of the anal region, the *Anisoptera* reveal much more primitive traits than the *Zygoptera*, whose wings were subject of very strong alteration»...

Basing on the Dollo's law of irreversibility of evolution, I considered to be impossible to derive the primitive and very plentiful wing-venation of *Anisoptera* from the very reduced venation of *Zygoptera*. Although *Anisoptera* were known from the deposits not older than the Upper Jurassic, I supposed they can be discovered in much older formations, perhaps, in palaeozoic ones. At present, such a hypothesis has found its demonstration in the discovery by M. Edemsky in the Permian of Iva-Gora, Archangelsk district, of the remains of wings, belonging to the stem of *Anisoptera*, although more primitive, than the recent representatives of this suborder.

Fam. **PERMAESCHNIDAE**, nova

Gen. **Permaeschna**, n. gen.

(Fig. 1—3)

Shape of wings as in recent *Anisoptera*, in *Aeschnidae*, especially. SC ending on C a little beyond the middle of wing; nodus absent, but the subnodus is present and placed at the middle of wing. R in the distal portion of wing

1 Sur l'interprétation de la nervation et de la trachéation des ailes des Odonates et des Agnathes Revue Russe d'Entomologie, XVIII, 1924, p. 157 (Russian). Also the translation (by F. Carpenter) of this paper in «Psyche», vol. 37, № 3, 1930.

running near to C, but slightly spaced from it in the region of pterostigma; pterostigma long, extending backwards, beyond the R, and forming an elongate thickening, not separated by any cross-veins. R dividing in the apical portion of pterostigma into two branches, posterior one running parallel to the upper branch of RS. RS long, as in *Anisoptera*, but dividing very late, just beyond the subnodus and forming two groups of branches, proximal and distal. Proximal group composed of RS_4, RS_5 and of «radial supplement» (Rspl), as usual in *Anisoptera*; it arises from the stem of RS, apparently, by a short common pedicel; distal group containing three branches, curved in S-shaped mode and circumambient the pterostigma; the stem of this group is united with R by a short, but distinct cross-vein; with RS_4 it is connected by several long cross-veins. At the end of RS_5 the margin of the wing is withdrawn somewhat deeper than in the recent *Anisoptera*. M also long and running near to RS, in the basal part of wing, probably, uniting with RS and then approximating to R. The region between convex MA and concave CuP is unusually large and filled up with two systems of branches and cells. The anterior group is united by a short pedicel with MA; posterior group is more composite and united by a cross-vein with the stem of M and by a feeble oblique vein with CuP. Comparison with *Calvertiella*, *Cockerelliella* and with some true *Palaeodictyoptera* (f. i. with *Microdictya*, *Eurythmopteryx*) shows that the distal group, corresponding clearly to the «Median supplement» (Mspl) of *Anisoptera*, is, morphologically, MP, while the basal (proximal) group, corresponding to the «trigonal supplement» of *Anisoptera*, or to the similar longitudinal vein between M and CuP in *Anisozygoptera*, represents CuA. However, this CuA is here already not distinctly convex, and MP not distinctly concave.

MP occupies in *Permaeschna*, as well as in *Anisoptera* and in *Anisozygoptera*, too distal position, but it is very probable that the stem of MP is somewhat shifted in *Anisoptera* distally; one may meet with the analogous distal branching of MP in some *Palaeodictyoptera* (*Eurythmopteryx*, some *Microdictya*) and even in the fam. *Meganeuridae*, subfam. *Typinae*.

In true *Anisoptera* and *Anisozygoptera* the area between MA and CuP is narrowed, and both these veins are subject to a more pronounced reduction, and, finally, disappear, their branches, with cross-veins, being metamorphosed in usual «odonatan» net.

The feeble vein, which runs obliquely from the cross-vein m-cu towards CuP, corresponds, in its position, to the outer edge of the triangle of *Aeschnidae*; one can consider it as the basal portion of CuA. Short cross-vein m-cu preserves in *Permaeschna* yet its original position and does not form a continuation of the outer edge of triangle. A_1 convex and running nearly parallel to CuP. Behind A_1 there is a second vein, feebly concave and nearly parallel to it; it represents, perhaps, A_2, but not in a primary condition. These veins are connected by single rows of cross-veins. Unfortunately, the basal portion of wings is not preserved.

Between C and SC exist but few distinct cross-veins; in the distal portion, between C and R, cross-veins are almost absent; between SC and R one may discern but 2—3 ones. Between R and RS_4 — several long and distinct cross-veins. The net in the region of the branches of RS (RS_3 — RS_5), of M and of CuA composed, mostly, of pentagonal cells, resembling those in *Anisoptera*.

Size, approximately, as in recent *Aeschnidae*.

In this genus are known two species:

1 (2) Both RS_2 and RS_3 simple and separate, RS_4 straight and separated from RS_3 by two rows of cells. — *Permaeschna dolloi*, n. sp.

2 (1) Rs_2 and Rs_3 united in their basal parts into a common pedicel, RS_{2+3}; some distal branches of RS_4 adjoined to RS_3. — *Permaeschna proxima*, n. sp.

Type of the genus — *Permaeschna dolloi* n. sp., from the Kasanian of Iva-Gora, Archangelsk district.

1. Permaeschna dolloi, n. sp.

(Fig. 1, 2)

Two impressions of a hind-wing; in the negative exemplar, № $^2/_{2334}$ (Fig. 1, 2), preserved the whole wing, without ist basal portion, in the positive exemplar preserved but the distal part of the wing.

The specimen represents, probably, a hind-wing.

Shape of the wing similar to that of the wings of *Anisoptera*, but somewhat narrower in the basal half. Distal portion, between the end of RS_5 and the apex, is, comparatively, short; on the contrary, the median portion, between CuP and RS_5, is unusually large.

Length of the preserved portion (fig. 2) 45 mm, that of the distal part — 13.5 mm; that between MA and CuP 22 mm; total length is about 55—56 mm; the breadth (in the basal part) — 14 mm. RS approximated

Fig. 1. Wing of *Permaeschna dolloi*, n. g. n. sp.; photograph.

to R in its distal portion. All three distal branches of RS separate, simple, connected by single rows of cross-veins; RS_4 almost straight, Rspl running parallel to it and forming about 8 short branches, forming rows of

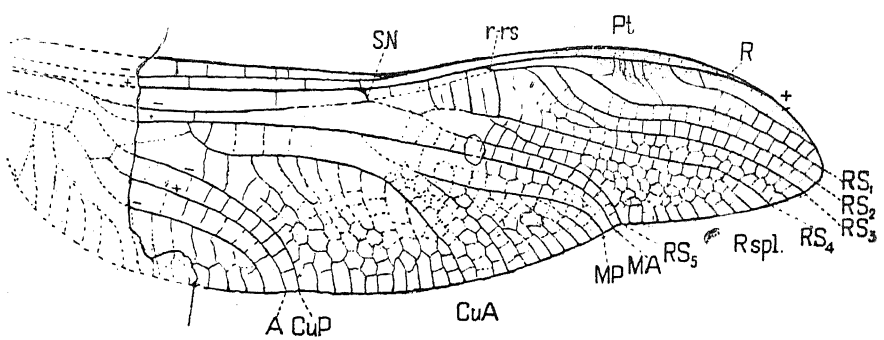

Fig. 2. Wing of *Permaeschna dolloi*, n. g. n. sp.

pentagonal and of hexagonal cells. MP connected with M at the level of the subnodus and forming 8 branches, CuA arcuate and forming about 9—10 similar, but longer branches. Outer edge of the triangle very oblique.

I allow to me to dedicate this species to Prof. Dr. L. Dollo, whose ideas always animated me in the researches in fossil Insects.

2. Permaeschna proxima, n. sp.

(Fig. 3)

Specimen № $^{4}/_{2334}$, representing distal ($^{2}/_{5}$) part of a wing. Similar to the foregoing species, differing, chiefly, by the second and third branches of RS united, in their basal portions, into a common short pedicel. Both rows of cells behind RS_3 and some few distal branches of RS_4 and of Rspl (in *P. Dolloi*) are adjoined here to RS_3, therefore the system of RS_4 + Rspl becomes more scarse. Between MA and MP a single row of distinct, long cross-veins. Pterostigma distinct, thickened, obscure, forming an arcuate proeminence backwards.

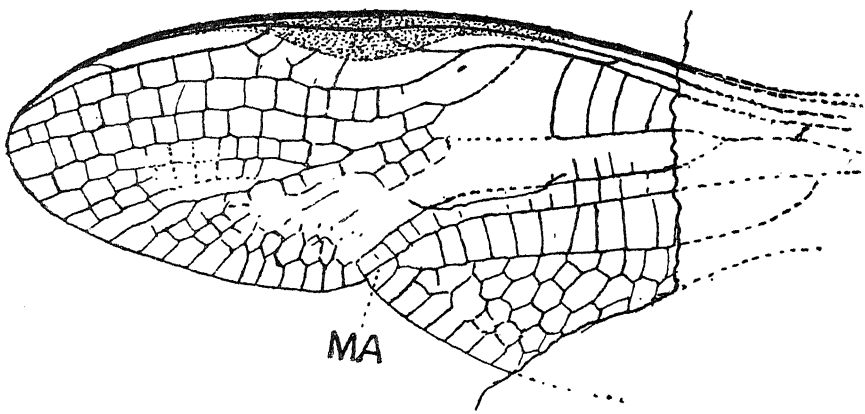

Fig. 3. Distal portion of the wing of *Permeschna proxima*, n. sp.

Length of the preserved portion 23 mm; breadth, near the excision at RS_5, 10.5 mm; total length should be the same as in *P. dolloi*.

By the shape of wings and by the general conformation of their venation the genus *Permaeschna* obviously resembles to *Anisoptera*, to some *Aeschnidae*, especially. Mesozoic *Anisozygoptera* are very diverse, but, nevertheless, they differ from *Permaeschna* more clearly than *Anisoptera*, and thus represent some early side-branches, separated from the common source of the stem of *Anisoptera*. They adopted some different ways of evolution; *Architemidae* in many traits remind already of *Zygoptera*, although they are not true *Zygoptera*. Although resembling to *Aeschnidae*, *Permaeschnidae* are much more primitive and possess also some peculiar

traits, for instance, the character of the distal branches of RS, which does not occur among true *Anisoptera*. They cannot be united with *Anisoptera* and should be separated into a distinct suborder, — *Protanisoptera* m.

Subordo PROTANISOPTERA nov.

Allied and similar to *Anisoptera* in the shape and venation of wings, but more primitive, differing from them, as follow: 1) nodus absent, SC ending on C beyond the middle of wing; 2) PT elongate, large, extending in the region between R and RS; 3) RS dividing very late, at the subnodus, and forming two groups of branches, of which 4) the distal group is composed of three simple curved veins; 5) the region between MA and CuP very large; 6) MP and, especially, CuA distinct and composite.

The primitivness of this suborder is evident from the features 1, 2, 3, 5 and 6.

The dividing of RS beyond the subnodus is, indeed, an archaic feature, shared also by the permian Zygopterous families, *Kennedyidae* and *Permagriidae*. Three distal branches of RS form, in many *Zygoptera*, a similar distal group, and RS_2 and RS_3 often derive from the stem of RS, as in *Permaeschna*.

The family *Permaeschnidae* may be characterised by the conformation of both groups of branches of RS, by the presence of a short cross-vein r-rs beyond SN, by relative size of MP and of CuA, by the presence of a concave anal vein behind A_1, and by some other features.

Being closely allied to *Anisoptera*, the suborder *Protanisoptera* reveals some primitive characters, reminding, for instance, of those in the gen. *Calvertiella* (*Protodonata*). This genus in the conformation of RS, of Cu and of anal region, as well as in the union of the composite anal vein with Cu, differs strongly from the fam. *Protagriidae* and, doubtless, should be separated into the distinct fam. *Calvertiellidae*, n. fam. The presence of separate MP and CuA is common to both these groups, but CuA in *Permaeschnidae* is more composite and MP is shifted in the distal direction. However, *Calvertiella* is more specialized in the anal region being united with Cu and in the absence of pterostigma. The plan of wing-venation in *Permaeschna*, compared with that in *Calvertiellidae*, *Cockerelliellidae*, *Protagriidae* and in some *Palaeodictyoptera*, necessitates us to propose some changing in the interpretation of the venation in *Anisoptera*. It is clear that MP and CuA

are not quite lacking in this group; they are represented by Mspl and by trigonal supplement, respectively; the outer edge of triangle represents, probably, the basal part of CuA. Thus, the stem of the *Anisoptera* proves, indeed, to be very old and archaic. It has originated, probably, directly from the more archaic *Palaeodictyoptera,* not from *Anisozygoptera* and, certainly, not from *Zygoptera* or from *Protozygoptera,* which were very similar to *Zygoptera.*

А. В. МАРТЫНОВ. О НЕКОТОРЫХ ЗАМЕЧАТЕЛЬНЫХ *ODONATA* ИЗ ПЕРМСКИХ ОТЛОЖЕНИЙ АРХАНГЕЛЬСКОГО РАЙОНА

РЕЗЮМЕ

В то время как стрекозы подотряда *Zygoptera* были давно известны из мезозоя, а в последнее время обнаружены и в пермских отложениях, стрекозы более крупного подотряда *Anisoptera* до сего времени были находимы лишь в отложениях не ниже верхней юры. Ввиду этого Тилльярдом было высказано (1928) определенное мнение, что *Anisoptera* не так древни и отделились от *Anisozygoptera* лишь в конце юры, а эти последние отделились от *Zygoptera.* Мною наоборот, отмечалась (1923) бо́льшая полнота, архаичность, а следовательно, и древность *Anisoptera.* Производить последних из *Zygoptera* мне казалось невозможным, потому что это противоречило бы закону Долло. Мои предположения оправдались фактом нахождения в пермских отложениях Ивы-Горы, Архангельской губ., остатков крыльев двух видов, несомненно, относящихся к ряду *Anisoptera.* Эти два вида относятся к одному роду *Permaeschna* m., выделяемому мною в особое семейство *Permaeschnidae* m. и в особый подотряд *Protanisoptera.* По строению жилкования и форме крылья этой группы уже очень близко напоминают крылья современных *Anisoptera,* но более примитивны и, кроме того, имеют и некоторые своеобразные особенности.

Узелка еще не было, и SC кончалась на C. RS делился поздно, на уровне подузелка, и давал пять ветвей, как у *Anisoptera,* но три дистальных ветви были изогнуты. Птеростигма велика и не отграничена. Задняя медиана (MP) и передний кубитус (CuA) имелись и были довольно сложны. Так называемые «добавочная медианы» (Mspl) и «добавочная треугольника» (Trgspl) стрекоз, очевидно, отвечают MP и CuA. Наружная сторона треугольника, по своему происхождению, есть начальная часть CuA. Эти черты жилкования *Permaeschnidae* заставляют сильно изменить обычную интерпретацию крыльев стрекоз; их структура стоит, по существу, гораздо ближе к таковой *Protodonata* и *Palaeodictyoptera,* чем это думали до сих пор.