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Studia nad muchówkami minującymi z rodziny *Agromyzidae* (*Diptera*). 2. Nowe przypadki rozwidlenia żyłki r_{2+3}, wyjaśnione jako zjawiska atawizmu

Исследования над минирующими двукрылыми из семейства *Agromyzidae* (*Diptera*). 2. Новые случаи разветления жилки r_{2+3} объясненные как явления атавизма

Studies on mining flies (*Diptera, Agromyzidae*). 2. Some new cases of bifurcation of vein r_{2+3}, interpreted as atavistic phenomena

[With 2 text-figures]

Cases of abnormal wing venation, consisting of shifting, deformation or atrophy of some veins or in development of additional ones, are known to occur in many dipterous families. In addition to references in numerous dipterological publications, there have been a number of special papers devoted to these phenomena. KRÖBER (1913) described and grouped venation anomalies in *Therevidae* and *Omphralidae*, in which they are particularly frequent. PIERRE (1918) reported some cases in *Tipulidae* and *Limnobiidae*. Venation anomalies of mining flies were described by HERING (1934), who established their presence in twenty species of *Agromyzidae* and in one species of *Anthomyidae*. HERING'S paper includes a number of generalizations and tentative interpretations of the facts observed. However, a majority of the theoretical conclusions was drawn by REINIG (1935); these conclusions were based on numerous variations in the wing venation of *Syrphidae*. JONES (1943) recorded one case in *Pollenia rudis* FBR. (*Cal-*

liphoridae). LINDNER (1949) in the general part of his collective work had devoted to venation anomalies a brief chapter in which he commented on the results obtained by KRÖBER and drew attention to the frequency of similar deviations in *Larvaevoridae*.

LINDNER (1949), as well as other authors dealing with abnormal wing venation of other insects, believes that only cases of very pronounced desorganization of the entire venation have the character of teratological changes due to physiological disturbances, caused either by hormonal factors or by parasites. Most authors are inclined to regard minor deviations, atrophy of single veins or parts thereof, and development of additional fragments as mutations or at any rate as changes that are genetic in nature. According to HERING (1934) the mutations may be induced by adverse enviromental effects on the larval instar or the diapausal stage; this would explain why the changes are more frequently met with in laboratory reared than in collected material.

Referring to KRÖBER'S results, LINDNER (1949) draws attention to the fact that although venation anomalies are not always symmetrical, there is, however, not infrequently a tendency towards similar variations in both wings at corresponding places. The frequency of this phenomena in a given family, or even species, warrants the supposition that a phylogenetic phase is in question. According to REINIG (1935), the individual mutability in the wing venation of *Syrphidae* concerns diagnostic characters of subspecies, species and higher taxonomic units, and the predominant tendency of the mutability is in agreement with the direction of the phylogenetical development. Deviations, though usually slight, are here very frequent, hypertrophies being definitely more common than atrophies. Additional fragments appear mostly in the arcs of the main veins near the alar margin and thus the veins are better fixed, thus strenghening the flight organ. Individual mutability is guided in a definite direction by natural selection continous perfecting of the wings of these well flying insects. Thus, after REINIG, venation „anomalies" represent in *Syrphidae* the normal pathway along which the evolution of wings is proceeding.

The interpretation referred to above cannot be applied to *Agromyzidae*. Comparing his results with HERING'S, REINIG himself observes that in these insects, which are relatively poor fliers having a more reduced venation, artophy is about as frequent as hypertrophy. As follows from HERING'S paper (1934), venation abnormalities are more pronounced, but less frequent, in the mining flies, and they usually involve characters constant within the family. Parallelism between individual variations and the general direction of group evolution can be noted only in cases of atrophy of some transverse veins, e. g. the *tp* vein. Where appearance of additional veins is in question, a distinction is to be drawn, above all else, between elements entirely new and those representing merely a reproduction of the ones that existed in preceeding phylogenetic phases. Phenomena of the first kind are difficult to trace owing to the possibility of shifts in the position of veins. An example may be found in the duplication of some transverse veins, e. g. of the *ta* vein. Phenomena of the second kind can be exemplified by the bifurcation of longitudinal veins normally single in *Agromyzidae*, but forked in their ancestors. HERING established four cases of bifurcation of vein r_{2+3}, two cases involving r_{4+5}, and four involving m_{1+2}.

Since bifurcations of longitudinal veins of the wing are rather rare in *Agromyzidae*, are opposed to the direction of evolution and are in conflict with characters constant within the group, thus reflecting past phylogenetic phases, they may be assumed with some likelihood to represent changes of the atavistic type. Atavisms in wing venation of insects may be used for phylogenetic investigations very much like other atavisms occuring in animals and plants. All the homologizations of the additional veins with the veins which were reduced in the course of the phyletic development are, however, uncertain owing to shiftings of longitudinal trunks. Obviously anomalies the atavistic character of which is after all uncertain cannot be considered as a proof for one or another phylogenetic hypothesis, but in any case such anomalies represent an indication or a secondary evidence.

HENNIG (1954), referring to „atavisms" in the wing venation of *Diptera*, writes of a reactivation or revival of a former

bed or track of a vein. Although he has in mind „atavisms" that have become stabilized as regular characters of a given species or higher taxonomic unit, nevertheless, his interpretation can be extended to atavisms having the character of anomalies, i. e. to individual deviations from specific characters.

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Working on *Agromyzidae* material collected in the Kampinos Forest near Warszawa, I met some new cases of anomaly in the venation of the radial field of the wing of these flies, with the bifurcation of vein r_{2+3}. This deviation existed in three reared specimens: in a male and a female from the hibernating generation of *Phytomyza aquilegiae* HARDY and in a male from the nonhibernating generation of *Phytomyza adjuncta* HER. The adults of *Ph. aquilegiae* HARDY I reared on May 11, 1956, from larvae mining the leaves of *Thalictrum minus* L. collected on July 23, 1955, east of the Zamczysko Reservation. The adult of *Ph. adjuncta* HER. was reared on July 19, 1957, from a larva mining a leave of *Pimpinella saxifraga* L., collected on July 5, at Łomna.

The venation anomaly consists of:

1) The forward pointing bend of vein r_{2+3} is more acute and apically somewhat thickened.

2) There is a slight and apically somewhat thickened backward bend in the costal vein opposite the bend in vein r_{2+3}.

3) In the first radial cell (R_1) there is on the underside of the wing an additional oblique vein connecting the vertex of the bend in r_{2+3} with the vertex of the opposite bend of the costal vein.

The anomaly appeared in the fully developed form just described only in the right wing of the female of *Ph. aquilegiae* HARDY and in the left wing of the male of *Ph. adjuncta* HER. In the female of *Ph. aquilegiae* HARDY there occurs, however, a very narrow, scarcely perceptible interruption between the additional vein and the thickened part of r_{2+3}, which thickening occurs about $^3/_4$ of the distance between the end of the radial sector and the costa [fig. 1a]. In the left wing

of the male of *Ph. adjuncta* HER. the fenomenon is reversed: the similar interruption occurs between the additional vein and the thickening of the costa. In the left wing of the female of *Ph. aquilegiae* HARDY only the costa is bend and thickened; the additional vein starting from it extends only half of the distance between c and r_{2+3} [fig. 1b]. In the right wing of

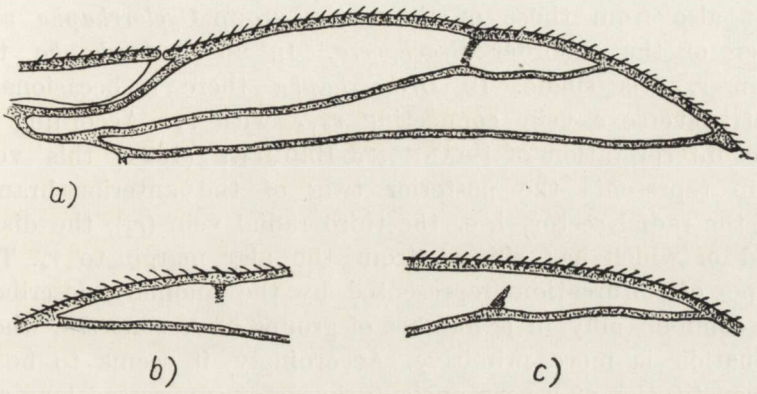

Fig. 1. Abnormally veined part of a wing of *Phytomyza aquilegiae* HARDY (authent. spec.) a) right wing ♀, b) left wing ♀, c) right wing ♂.

the male of this species the phenomenon is reversed: there is only an apical thickening of the bend in r_{2+3} and this thickening is $^2/_3$ of the distance between the end of r_s and the costa, whereas the additional vein starting from it extends only half of the length [fig. 1c]. The left wing of the male of *Ph. aquilegiae* HARDY and the right one of the male of *Ph. adjuncta* HER. are normally veined.

This deviation is thus reproducible since it was observed in three specimens, a female and two males, belonging to two unrelated species, and it is partially symmetrical.

The appearance of fragments of the additional vein, now from the side of the anterior branch of the radial sector, now from the side of the costa, is indicative of a tendency towards reactivation of some former track connecting the two longitudinal trunks. Owing to the reactivation of the track, the anterior branch of the sector forks forming two twigs, the anterior one (the additional vein) corresponding to the second radial vein (r_2), and the posterior one (section r_{2+3} between

point of bifurcation and alar margin) corresponding to the third radial vein (r_3). These twigs, together with the section of the costa included between their distal ends, define an additional wing cell which could be called second radial cell (R_2). Bifurcation of the central branch of the radius, with both twigs reaching the alar margin, amounts to a deviation from not only the characters of the family *Agromyzidae*, but also from those of the entire group *Cyclorrhapha* and even of the suborder *Brachycera*. In all *Cyclorrhapha* the vein r_{2+3} is single. In *Orthorrhapha* there is occasionally a transverse s vein connecting r_{2+3} with r_4. According to the interpretation of SHANNON & BROMLEY (1924) this very vein represents the posterior twig of the anterior branch of the radial sector, i. e. the third radial vein (r_3), the distal end of which has shifted from the alar margin to r_4. The type of bifurcation represented by the anomaly described, is common only in a number of groups of *Nematocera*, where venation is more primitive. Accordingly it seems to be a reconstitution of a very ancient character suppressed long ago in the course of the phyletic development.

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The instance of atavism described, as well as cases described by HERING not only seems to indicate the existance of bifurcation in the anterior branch of the radial sector in the ancestors of *Cyclorrhapha*, but also to show how this bifurcation came to disappear. For, since in all the deviations noted the aditional vein represents the anterior twig of the branch in question, i. e. the second radial vein (r_2), it must have been exactly this vein that has become atrophied in the course of the phyletic development.

The homologization of the additional vein described with r_2 although attractive enough, is, however, doubtful.

It is generally agreed that the primitive, most generalized type of wing venation in *Diptera*, at least of the radial field, does not differ appreciably from that of the hypothetical primitive wing of *Pterygota*, as advanced by COMSTOCK & NEEDHAM (1898, 1899). In this primitive wing the radial trunk divides in the first radial vein (r_1) and the radial sector (r_s),

the latter producing by two-fold dichotomy further radial veins: r_2, r_3, r_4 and r_5 — all reaching like r_1 the alar margin. This type of radial field venation with the quadrifurcate radial sector is still retained in the primitive *Nematocera* of the family *Tanyderidae*, e. g. *Protoplasa fitchii* O. S. [fig. 2]. The evo-

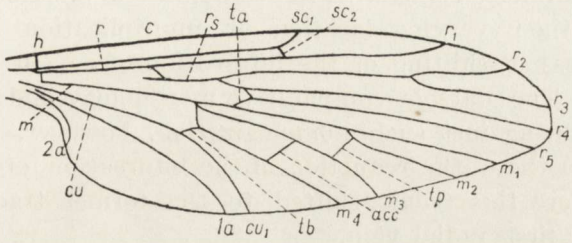

Fig. 2. Wing venation of *Protoplasa fitchii* O. S. (*Tanyderidae*) (after HENNIG, 1954, changed).

lution from the quadrifurcate radial sector of the most primitive *Nematocera* to the triple and subsequently bifurcate sector of *Brachycera* is due to progressive reduction involving first trunk r_{2+3} and then trunk r_{4+5}, i.e. by fusion of r_2 with r_3 and then r_4 with r_5 or, alternatively, by atrophy of one out of either two pairs of veins.

But the evolution of the radial field of the wing of *Brachycera* also consisted in a translocation of the longitudinal trunks towards the anterior margin of the wing, together with a shifting of their distal ends towards the basis of the wing. In the primitive form of *Diptera* [cf. fig. 2] the twigs of r_{4+5} reach just beyond the apex of the wing, the twigs of r_{2+3} just before the apex, and r_1 also ends considerably nearer the apex than the basis of the wing. In *Agromyzidae* r_{4+5} ends just before the apex of the wing, while r_{2+3} runs in its distal portion almost along a line drawn a prolongation of r_1. The branch r_1 is limited to the basal part of the wing.

Since the trunk r_{2+3} being shifted anteriorly runs almost along the distal part of the former track of r_1, the oblique additional vein connecting r_{2+3} with the anterior margin of the wing occupied by the costa seems to be more a reconstitution of the former very terminal portion of r_1 than a re-

constitution of r_2. The appearance of such additional veins at varying distances from the basis of the wing, sometimes even in one individual (cf. HERING, 1934; HENNIG, 1954) would seem to be a recapitulation of various phases of the evolutionary process of contraction of r_1. In homologizing these additional veins with r_2, we ought to be able to perceive in their varying location or multiplication traces of the process of shifting of the bifurcation of r_{2+3} in the distal direction. The data of comparative morphology and paleontology argue against such homologization, however, since according to these the reduction of the bifurcation of r_{2+3} took place before this trunk shifted to the former track of the shortened first radial vein.

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STRESZCZENIE

Autor opisuje przypadek nienormalnego użyłkowania skrzydła u trzech wyhodowanych przez siebie okazów muchówek należących do dwu niespokrewnionych ze sobą gatunków: *Phytomyza aquilegiae* HARDY (♂ i ♀) oraz *Phytomyza adjuncta* HER. (♂). Anomalia polega przede wszystkim na pojawieniu się dodatkowej, skośnie biegnącej żyłki, która łączy r_{2+3} z przednim brzegiem skrzydła zajętym przez żyłkę kostalną. Żyłka dodatkowa jest wykształcona prawie zupełnie jedynie w prawym skrzydle samicy *Ph. aquilegiae* HARDY oraz w lewym skrzydle samca *Ph. adjuncta* HER. W lewym skrzydle samicy *Ph. aquilegiae* HARDY występuje tylko przednia połowa żyłki dodatkowej połączona z żyłką kostalną, zaś w prawym skrzydle samca tego gatunku tylko połowa tylna połączona z r_{2+3}. Lewe skrzydło samca *Ph. aquilegiae* HARDY oraz prawe skrzydło samca *Ph. adjuncta* HER. mają użyłkowanie normalne.

Dzięki pojawieniu się tej dodatkowej żyłki przypominającej żyłkę radialną drugą (r_2) przednie ramię sektora radialnego czyli żyłka r_{2+3}, która u wszystkich *Cyclorrhapha* jest pojedyncza, uzyskuje postać rozwidloną, jaka istniała u dalszych przodków tej grupy i zachowała się jeszcze wśród współczesnych prymitywnych muchówek. Podobne przypadki bifurkacji r_{2+3}, jak również r_{4+5}, obserwował już u *Agromyzidae* HERING (1934). Ponieważ anomalie te są rzadkie, niezgodne z kierunkiem ewolucji grupy, naruszają cechy niezmienne w jej obrębie i nawiązują do minionych faz rozwoju rodowego, autor przypuszcza, iż są to zmiany typu atawistycznego, które mogą być wykorzystywane do wniosków filogenetycznych. Nasuwająca się sama przez się homologizacja żyłki dodatkowej z r_2 nie byłaby jednak uzasadniona, ponieważ r_{2+3}, na skutek przesunięcia się ku przedniemu brzegowi skrzydła, przylega do części dawnego toru skróconej r_1. Żyłka dodatkowa odtwarza więc raczej dawny końcowy odcinek żyłki radialnej pierwszej, która w minionych fazach rozwoju rodowego sięgała znacznie dalej w kierunku ku wierzchołkowi skrzydła.

РЕЗЮМЕ

Автор описывает случай аномалии жилкования крыла у трех выведенных им экземпляров минирующих двукрылых принадлежащих к двум неродственным видам: *Phytomyza aquilegiae* Hardy и *Phytomyza adjuncta* Her. Аномалия прежде всего состоит в присутствии добавочной, косо пробегающей жилки, которая соединяет r_{2+3} с передним краем крыла, занятым костальной жилкой. Добавочная жилка почти совсем оформлена только на правом крыле самки *Ph. aquilegiae* Hardy и на левом крыле самца *Ph. adjuncta* Her. На левом крыле самки *Ph. aquilegiae* Hardy находится только передняя половина добавочной жилки, соединенная с костальной жилкой, зато на правом крыле самца этого вида только задняя половина соединенная с r_{2+3}. На левом крыле самца *Ph. aquilegiae* Hardy и на правом крыле самца *Ph. adjuncta* Her. жилкование нормальное.

Благодаря присутствию этой добавочной жилки, напоминающей вторую радиальную жилку (r_2), передняя ветвь радиального сектора или жилка r_{2+3}, которая у всех *Cyclorrhapha* является единичной, приобретает раздвоенный вид, какой был у отдаленных предков этой группы и сохранился еще среди настоящих примитивных двукрылых. Подобные случаи бифуркации r_{2+3}, равно как r_{4+5}, наблюдал уже Геринг (1934). Так как эти аномалии редки, не соответствуют направлению эволюции группы, нарушают признаки постоянные у ее представителей и напоминают прежние фазы ее эволюционного развития, автор предполагает, что это отклонения атавистического характера, которые могут быть использованы для филогенетических выводов.

Кажущаяся очевидной гомологизация добавочной жилки с r_2, однако сомнительна, так как r_{2+3} вследствие перемещения к переднему краю крыла прилегает к части прежнего пути сокращенной r_1. Таким образом добавочная жилка воспроизводит скорее прежний концевой участок первой радиальной жилки, которая на минувших этапах родового развития доходила значительно дальше по направлению к вершине крыла.

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