HOMOLOGY OF SUBMARGINAL CROSSVEINS IN FOREWINGS OF BEES (Hymenoptera: Apiformes)

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Summary

In the forewings of bees (Apiformes) there are either two or three submarginal cells. In the case of wings with two submarginal cells it is not clear if the remaining crossvein separating the cells is homologues with the first or the second submarginal crossvein. Information about homology of the crossveins is important for reconstructing phylogenies of bees. I attempted to determine the homology of the submarginal crossveins using quantitative methods. Coordinates of 14 vein junctions were superimposed to determine the expected position of the submarginal crossveins. It was expected that distribution of the position of the remaining crossveins in wings with two submarginal cells would be similar to the combined distribution of the first and second crossvein in wings with three submarginal cells. However, the distributions differed markedly between wings which had two or three submarginal cells. The position of the remaining crossvein was often between the expected position of the first and second submarginal crossvein. Moreover, the distribution of the remaining crossvein was bimodal, which confirms earlier suggestions that both the first and second submarginal crossvein may be lost in evolution. The results suggest that in bees there are patterns of wing venation which are preferred by natural selection. Similar patterns can be a result of the disappearance of either the first or second submarginal crossvein. This makes the reconstruction of remaining crossvein homology difficult.

Keywords: bees, Apiformes, wing, venation, submarginal crossvein, homology.

INTRODUCTION

Almost all bees (Apiformes) share a characteristic venation pattern. Only in Meliponini, Neolarrini, Allodapini, and Euryglossinae can the venation be reduced at the distal part of the wing (Michener, 2000). Within the characteristic pattern, there are two major types of venation with two or three submarginal cells. Those two patterns result from the loss of either the second abscisa of Rs (2nd Rs) or first r-m (1r-m). Following terminology of Michener (2000), the two veins are called here; first and second submarginal crossveins. For the sake of brevity in this paper, I often skip the word "submarginal" and use the terms: "first crossvein" and "second crossvein". In the case of wings with two submarginal cells, the crossvein separating the cells is called the "remaining crossvein". This terminology should not be misleading, as I do not take into consideration here any other crossveins than the submarginal. In older literature, the crossveins were called transverse cubital veins (Robertson, 1926) or radiomedial veins (Louis, 1973).

In evolution, the submarginal crossveins were lost independently in many systematic groups. In at least 6 families (Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae, Melittidae) there are species with both two and three submarginal cells. Even in some genera (e.g. *Epeolus*, *Eucera*, *Lasioglossum*, *Leioproctus*, *Nomada*, *Rhopalolemma*, *Sphecodosoma*) there are species with two or three submarginal cells. Within species, all individuals usually have either two or three submarginal cells. Only occasionally

there are individuals with unusual venation. In bees with three submarginal cells (e.g. *Andrena*, *Halictus*, *Lasioglossum*, *Melecta*, *Nomada*, *Sphecodes*), either the first or the second crossvein was found missing (Peters, 1969). In honeybees, the second submarginal crossvein is sometimes incomplete (Alpatov, 1928). In *Eucera* and *Pseudopanurgus*, there are normally two submarginal cells but occasionally there are three of them (Robertson, 1922; Peters, 1969). The unusual venation is more common in males (Peters, 1969). Michener (2000, p. 105) suggested that a submarginal crossvein can disappear in a taxonomic group because some genes are inactivated and later in evolution the crossvein can appear again when the genes are activated. It is not clear if the number of submarginal cells has any adaptive value. It has been suggested, that the loss of the crossveins can be related to smaller size (Peters, 1969) and parasitism (Robertson, 1926).

When there are two submarginal cells, it is often not clear which of the two submarginal crossveins is missing. This information could be important for the reconstruction of phylogenies. In the past, the relative size of submarginal cells was used to predict which crossvein is missing. If the first submarginal cell was significantly longer than the second, it was suggested that the first crossvein was lost. However, in some cases the difference between the submarginal cells is small. Micherner (2000) suggested that in Hylaeinae, in most cases, the first crossvein is missing. In some genera, for example *Hyleoides,* it is impossible, however, to determine which crossvein is missing. On the other hand, it was suggested that in most Panurginae, the second submarginal crossvein was lost (Robertson, 1922).

The methods used so far for determination of homology of the remaining crossvein were to a large degree, arbitrary, and were applicable only in rare occasions when the difference between submarginal cells was large. The aim of this study was to use quantitative methods in order to determine the homology of submarginal crossveins in forewings of bees. Using the position of some veins (homology of which is known), the position of the remaining crossvein was calculated and compared with the expected position of the first and second crossvein. It was expected that the distribution of the position of the remaining crossveins would be similar to the combined distribution of the first and second crossveins.

MATERIAL AND METHODS

In the analysis, forewings of 119 species of bees were used. The species represent a wide range of systematic groups: 7 families, 19 subfamilies and 115 genera. No more than one species was used from one subgenus. There were 47 wings with two submarginal cells (Tab. 1), and 72 wings with three submarginal cells. The analysed species with three submarginal cells were: *Agapostemon texanus* Cresson, *Ancyloscelis panamensis* Michener, *Andrena* (*Callandrena*) *accepta* Viereck, *Anthophora occidentalis* Cresson, *Anthrenoides meridionalis* (Schrottky), *Apis mellifera* Linnaeus, *Augochlora pura* (Say), *Augochlorella striata* (Provancher), *Augochloropsis metallica* (Fabricius), *Bombus pennsylvanicus* (Degeer), *Cadeguala albopilosa* (Spinola), *Caenonomada bruneri* Ashmead, *Callomelitta picta* Smith, *Canephorula apiformis* (Friese), *Caupolicana hirsuta* (Spinola), *Centris* (*Centris*) *poecila* Lepeletier, *Ceratina dupla* Say, *Chalepogenus caeruleus* (Friese), *Chrysocolletes moretonianus* (Cockerell), *Colletes* sp. Latreille, *Deltoptila montezumia* (Smith), *Diadasia afflicta* (Cresson), *Dieunomia nevadensis* (Cresson), *Diphaglossa gayi* Spinola, *Doeringiella* (*Triepeolus*) *verbesinae* (Cockerell), *Epeoloides coecutiens* (Fabricius), *Epeolus cruciger* Panzer, *Epicharis* (*Epicharana*) *elegans* Smith, *Euglossa cordata* (Linnaeus), *Exaerete smaragdina* (Guérin-Méneville), *Exomalopsis* (*Exomalopsis*) *zexmeniae* Cockerell, *Habralictus trinax* (Vachal), *Homalictus dampieri* (Cockerell),

Table 1.

Classification of the remaining crossvein in forewings of bees as the first or second submarginal crossvein; classification should be interpreted carefully especially in cases where posterior classification probability P is low.

Family	Subfamily	Species	Classification of crossvein	P
Colletidae	Coletinae	*Leioproctus* (*Filiglossa*) *filamentosus* (Rayment)	first	0.993
		Scrapter nitidus (Friese)	second	0.509
	Xeromelissinae	*Chilicola* (*Anoediscelis*) *ashmeadi* (Crawford)	second	0.999
	Hylaeinae	*Hylaeus* (*Heterapoides*) *extensus* (Cockerell)	second	0.977
		Hyleoides concinna (Fabricius)	first	0.972
	Euryglossinae	*Euhesma goodeniae* (Cockerell)	second	0.997
		Euryglossa subsericea Cockerell	second	0.605
		Hyphesma atromicans (Cockerell)	second	0.999
		Xanthesma furcifera (Cockerell)	second	0.999
Andrenidae	Panurginae	*Calliopsis* (*Calliopsis*) *andreniformis* Smith	first	0.982
		Calliopsis (*Hypomacrotera*) *subalpina* Cockerell	first	0.753
		Callonychium minutum (Friese)	first	0.795
		Camptopoeum friesei Mocsáry	first	0.999
		Macrotera (*Macrotera*) *bicolor* Smith	second	0.997
		Panurginus occidentalis (Crawford)	second	0.995
		Panurgus calcaratus (Spinola)	first	0.998
		Perdita (*Callomacrotera*) *acapulconis* Timberlake	second	0.975
		Perdita (*Perdita*) *chihuahua* Timberlake	second	0.999
		Protandrena (*Heterosarus*) *neomexicana* (Cockerell)	first	0.999
		Pseudopanurgus aethiops (Cresson)	first	0.999
Halictidae	Rophitinae	*Dufourea marginata* (Cresson)	first	0.999
		Micralictoides altadenae (Michener)	first	0.967
	Halictinae	*Lasioglossum* (*Hemihalictus*) *lustrans* (Cockerell)	first	0.999
Melittidae	Dasypodainae	*Dasypoda Panzeri* Spinola	second	0.999
		Hesperapis pellucida Cockerell	second	0.985
	Melittinae	*Macropis europaea* Warncke	first	0.930
Megachilidae	Fideliinae	*Pararhophites orobinus* (Morawitz)	second	0.598
	Megachilinae	*Anthidium manicatum* (Linnaeus)	second	0.972
		Anthodioctes gualanense (Cockerell)	first	0.673
		Ashmeadiella bucconis (Say)	first	0.905
		Atoposmia (*Hexosmia*) *copelandica* (Cockerell)	first	0.999
		Dioxys productus subruber (Cockerell)	second	0.999
		Megachile chrysopyga Smith	second	0.863
		Paranthidium jugatorium perpictum (Cockerell)	first	0.658
		Trichothurgus dubius (Sichel)	second	0.894
Apidae	Xylocopinae	*Allodape interrupta* Vachal	first	0.892
		Compsomelissa (*Compsomelissa*) *nigrinervis* (Cameron)	second	0.999
		Macrogalea candida Smith	second	0.999
		Nasutapis straussorum Michener	second	0.816
	Nomadinae	*Biastes brevicornis* (Panzer)	first	0.999
		Caenoprosopis crabronina Holmberg	second	0.999
		Holcopasites heliopsis (Robertson)	second	0.999
		Rhopalolemma Robertsi Roig-Alsina	second	0.999
		Townsendiella californica Michener	second	0.999
	Apinae	*Anthophorula* (*Anthophorula*) *compactula* Cockerell	first	0.999
		Ctenoplectra sp. Kirby	first	0.999
		Eucera chrysopyga Pérez	first	0.997

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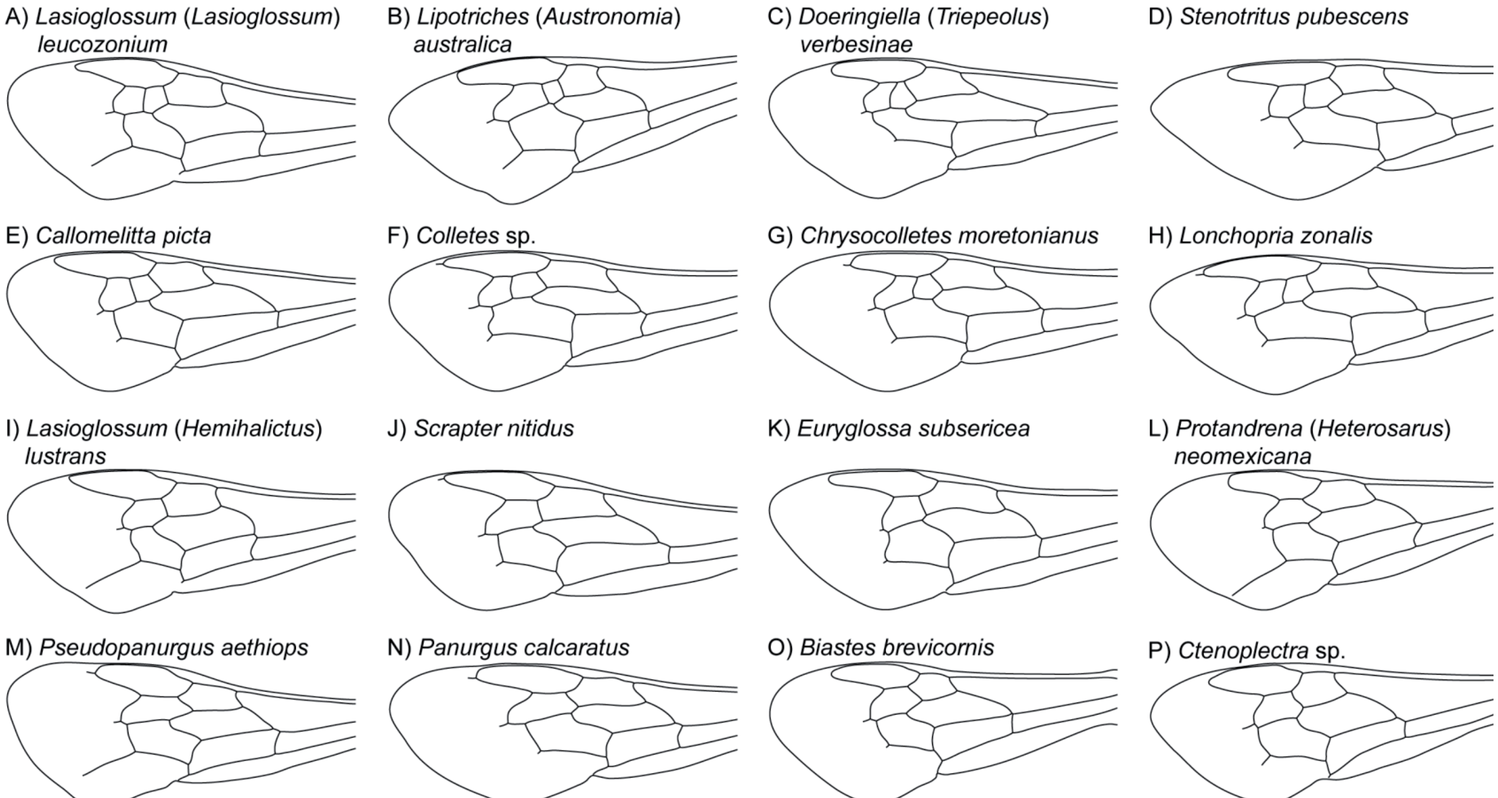

Fig. 1. Forewings of bees with three submarginal cells (A-H) and two submarginal cells (I-P); the images are not drawn to the same scale (redrawn from Michener, 2000).

Isepeolus viperinus (Holmberg), *Lasioglossum* (*Lasioglossum*) *leucozonium* (Schrank), *Leiopodus lacertinus* Smith, *Leioproctus* (*Protomorpha*) *tarsalis* (Rayment), *Lipotriches* (*Austronomia*) *australica* (Smith), *Lonchopria zonalis* (Reed), *Megalopta genalis* Meade-Waldo, *Megandrena enceliae* (Cockerell), *Meliltturga clavicornis* (Latreille), *Melissodes agilis* Cresson, *Melissoptila* (*Ptilomelissa*) sp. Moure, *Melitta leporina* (Panzer), *Mesocheira bicolor* (Fabricius), *Mesonychium garleppi* (Schrottky), *Microshecodes truncaticaudus* Michener, *Mydrosoma bohartorum* Michener, *Neofidelia profuga* Moure and Michener, *Nomada annulata* Smith, *Nomia* (*Acunomia*) *melanderi* Cockerell, *Nomioides minutissimus* (Rossi), *Odyneropsis* sp. Schrottky, *Osiris* sp. Smith, *Paranomada velutina* Linsley, *Paratetrapedia calcarata* (Cresson), *Parepeolus niger* Roig-Alsina, *Psaenythia bergi* Holmberg, *Pseudagapostemon* sp. Schrottky, *Ptiloglossa guinnae* Roberts, *Ptilothrix fructifer* (Holmberg), *Sphecodes gibbus* (Linnaeus), *Stenotritus pubescens* (Smith), *Systropha curvicornis* (Scopoli), *Tetrapedia* sp. Klug, *Thygater analis* (Lepeletier), *Trichocolletes venustus* (Smith), *Trigonopedia* sp. Moure, *Xeromelecta* (*Melectomorpha*) *californica* (Cresson), *Xylocopa tabaniformis orpifex* Smith, and *Zacosmia maculata* (Cresson).

The wing images (Fig. 1) were obtained from the comprehensive book of Michener (2000). The images were scanned using the HP Scanjet 5590 flatbed scanner with a resolution of 600 dots per inch. Venation of the wings was compared using landmarks located at wing vein junctions (Gerula et al., 2009; Szymula et al., 2010). In wings with two and three submarginal cells, coordinates of 16 and 18 vein junctions (Fig. 2), respectively, were determined using tpsDig software (Rohlf, 2005). The coordinates were superimposed using the Procrustes method (Rohlf and Slice, 1990). The superposition was based on vein junctions 1-14, the homology of which is known. However, in each wing, all 18 (or 16, in the case of wings with two submarginal

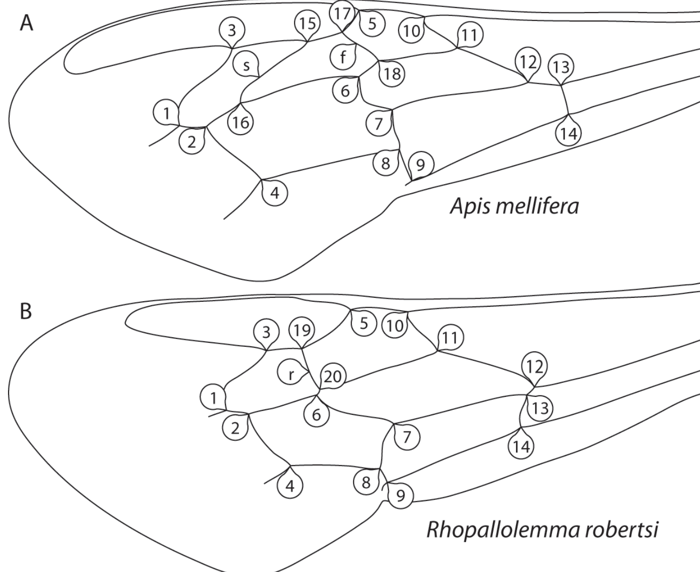

Fig. 2. Forewings of bees with three submarginal cells (A) and two submarginal cells (B). The vein junctions are numbered with consecutive numbers. Letters indicate submarginal crossveins: f - first submarginal crossvein, s - second submarginal crossvein, r - remaining submarginal crossvein.

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cells) were translated, scaled, and rotated in the same way. By doing this, the expected position of the submarginal crossveins was determined in relation to the rest of the venation (Fig. 3). The wing diagrams presented in Fig. 1 and 2 were produced using DrawWing version 0.12 (Tofilski, 2004). Discriminant function analysis was used to classify the crossveins as the first or second submarginal crossvein. The discriminant analysis was based on four variables: two coordinates of anterior endpoint and two coordinates of posterior endpoint of crossveins.

In order to compare the size of bees with two and three submarginal cells, the midrange of body length was used. The midrange was calculated as the sum of the minimum and maximum values, divided by two. The minimum and maximum values for most genera and subgenera were obtained from Michener (2000). In two cases (*Andrena* (*Callandrena*) and *Epeolus*), the range was not provided in the book and the two cases were excluded from the analysis of size.

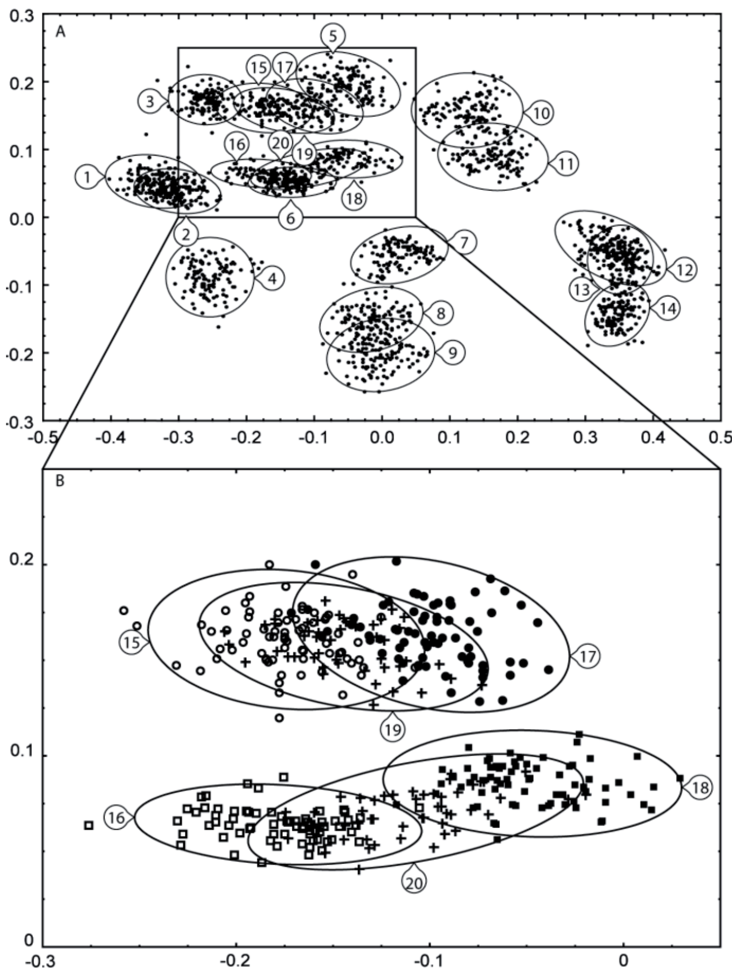

Fig. 3. Superimposed vein junctions of bee forewing (A) and enlarged fragment showing only junctions 15-20 corresponding to submarginal crossveins (B). The numbers of the junctions are the same as in Fig. 2. Ellipses indicate area in which the vein junctions can be expected with a probability 0.95.

RESULTS

After superposition most of the vein junctions of bee wings formed well separated clusters (Fig. 3A). The clusters corresponding to different vein junctions overlapped to some degree if distance between the junctions was small. This is particularly visible in junctions 12 and 13, which in evolution markedly changed their position (Fig. 2).

In wings with three submarginal cells, the first and second crossveins were relatively well separated, especially, at the posterior ends (junctions 16 and 18; Fig. 3B, 4AC). The coordinates of the endpoints differed significantly between the first and second crossveins (MANOVA: Wilks Lambda=0.126; F=240.1; P<0.001). In univariate comparisons only the y-coordinate of anterior ends (junctions 15 and 17) did not differ significantly between the two crossveins.

In wings with two submarginal cells, the anterior endpoint of the remaining crossvein formed a single cluster rather than the two expected clusters. The distribution of the x-coordinate of the anterior endpoint (junction 19) of the remaining crossvein was unimodal (Fig. 4B). The posterior endpoint (junction 20) of the remaining crossvein also formed a single cluster, however, in this case the distribution of x-coordinate was bimodal. The two maxima of the distribution (Fig. 4D) did not match corresponding maxima of either the first or the second crossvein (Fig. 4C). The combined distribution of the x-coordinate of the first and second crossvein was significantly different from the distribution of the x-coordinate of the remaining crossvein in the case of both the anterior and posterior endpoint (Chi-square: χ^2=76.2, P<0.001; χ^2=146.6, P<0.001, respectively).

Discriminant analysis based on resubstitution correctly classified as the first or the second crossvein most (98.6%) crossveins of wings with three submarginal cells. Out of 72 wings with three submarginal cells, two were classified incorrectly. In *Lipotriches* (*Austronomia*) *australica* wing (Fig. 1B) the second crossvein was classified as the first and in *Doeringiella* (*Triepeolus*) *verbesinae* wing (Fig. 1C), the first crossvein was classified as the second. Discrimination functions obtained from the discriminant analysis were used to classify the remaining crossveins from wings with two submarginal cells. Out of 47 remaining crossveins, 22 (46.8%) and 25 (53.2%) were classified as the first and second crossvein, respectively (Tab. 1).

Bee genera and subgenera with two submarginal cells were significantly smaller than bee genera and subgenera with three submarginal cells (Student's t-test: t=5.62; N_1=70; N_2=47; P<0.001). The average body length of bees with two and three submarginal cells was 7.7 and 11.2 mm, respectively.

DISCUSSION

The results clearly show that position of the remaining submarginal crossveins in bees wings with two submarginal cells is markedly different than the position of either the first or the second crossveins in wings with three submarginal cells. The endpoints of the remaining crossveins do not form separate clusters corresponding to either the first or the second submarginal crossvein, as it was expected. The second crossvein moved basad if the first was lost and the first crossvein moved apicad if the second was lost. In this situation, reconstruction of homology of the remaining crossveins is difficult and imprecise. The presented here classification of the remaining crossveins as homologues with the first or second submarginal crossvein should be interpreted carefully. Not only in *Hyleoides* is it not clear which crossvein is missing (Michener, 2000) but also in many other genera (Tab. 1).

The distribution of the x-coordinate of the posterior end of the remaining crossvein is bimodal (Fig. 4D). This confirms the earlier suggestions that both the first and second crossvein can be lost during evolution (Peters, 1969). There are two possible evolutionary scenarios leading to the

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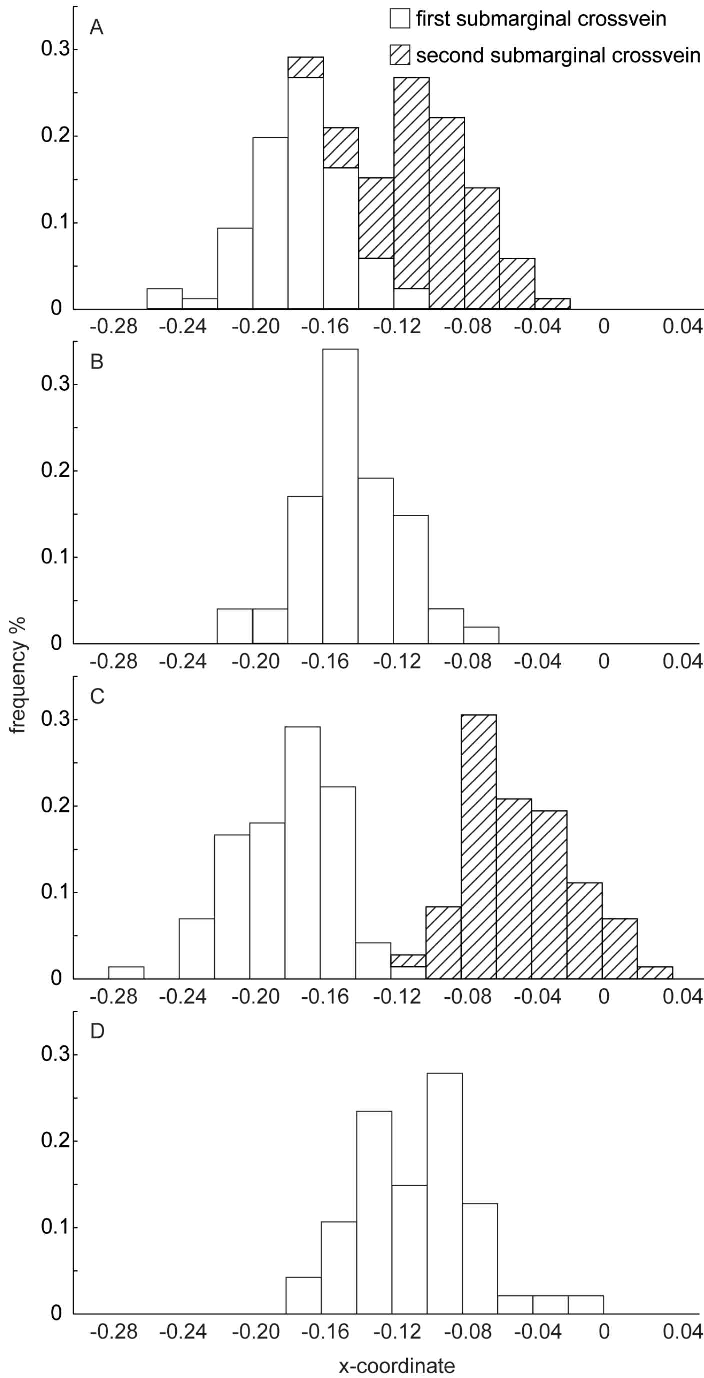

Fig. 4. Distribution of x-coordinates of endpoints of submarginal crossveins. Graphs A and B correspond to anterior ends of the crossveins; graphs C and D correspond to posterior ends of the crossveins; graphs A and C correspond to wings with three submarginal cells and graphs B and D correspond to wings with two submarginal cells.

current position of the remaining crossvein. The first scenario is that earlier in evolution, one of the crossveins was lost leading to one large and one small submarginal cell. Later, the remaining crossvein moved in such a way that the disproportion of cell sizes was reduced. The second scenario is that earlier in evolution, two crossveins moved in such a way that there were three submarginal cells of unequal sizes and later, one of the crossveins was lost leading to two submarginal cells of similar sizes (Robertson, 1926). Disappearance of the crossveins can either be sudden, as it sporadically happens in *Halictus* (Peters, 1969), or gradual like in *Lasioglossum* (Michener, 2000).

In some studies, it was assumed that differences in wing venation are proportional to phylogenetic differences and they were used for reconstructions of phylogenies (Dietrich et al., 2001). The results presented here suggest that in bees, the positions of the crossveins are not independent of each other and natural selection favours some patterns of veins. Therefore, wings with similar venation can be a result of convergent evolution (Sharkey and Roy, 2002). Shape of venation can affect fitness because veins are important for wing stiffness and in consequence, for flight performance (Combes and Daniel, 2003). On the other hand, there is evidence that in honeybees (*Apis mellifera*), variation of wing venation present in natural populations does not affect fitness (Diniz-Filho et al., 1999).

The loss of one of the crossveins can be related to size. Bees with three submarginal cells are on average, larger than bees with two submarginal cells. Comparison of subgenera within some genera confirms this. The genus *Eucera* subgenus *Synhalonia* with the largest bees, has three submarginal cells, and the other subgenera with smaller bees have two submarginal cells. Genus *Leioproctus* subgenus *Filiglossa* with the smallest bees has two submarginal cells while most other subgenera with larger bees have three submarginal cells. Moreover, bees with incomplete venation (e.g. *Brachyhesma*, *Euryglossina*, *Euryglossula*, *Neolarra*) tend to be smaller than bees with full venation. It is well known that smaller insects have reduced venation (Peters, 1969; Chapman, 1998). The reduction can range from loss of distal veins (Danforth, 1989) to loss of almost all veins, as in Chalcidoidea (Gauld and Bolton, 1988).

CONCLUSIONS

1. The data presented here suggest that in bees there are patterns of wing venation which are preferred by natural selection. Similar patterns can be a result of the disappearance of either the first or the second submarginal crossvein. In this situation, it is difficult to determine homology of the veins using their position alone.
2. Genera with three submarginal cells tend to be larger than bees with two submarginal cells.

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HOMOLOGIA ŻYŁEK SUBMARGINALNYCH PRZEDNICH SKRZYDEŁ PSZCZÓŁ (Hymenoptera: Apiformes)

Tofilski A.

Streszczenie

Na przednich skrzydłach pszczół (Apiformes) znajdują się dwie lub trzy komórki submarginalne. W przypadku skrzydeł z dwoma komórkami submarginalnymi nie wiadomo czy żyłka oddzielająca te dwie komórki (zwana dalej żyłką problematyczną) jest homologiczna z pierwszą czy drugą żyłką submarginalną. Poznanie homologii tej żyłki jest ważne w przypadku odtwarzania filogenezy pszczół. Podjęto próbę określenia homologii problematycznej żyłki używając metod ilościowych. Współrzędne 14 połączeń żyłek przedniego skrzydła nałożono na siebie w celu określenia położenia żyłek oddzielających komórki submarginalne. Oczekiwano, że rozkład położenia problematycznej żyłki będzie podobny do połączonych rozkładów położenia pierwszej i drugiej żyłki submarginalnej. Wbrew oczekiwaniom okazało się, że problematyczna żyłka znajduje się często pomiędzy oczekiwanym położeniem pierwszej i drugiej żyłki submarginalnej. Rozkład położenia problematycznej żyłki był dwumodalny, co potwierdza wcześniejsze sugestie, że zarówno pierwsza jak i druga żyłka submarginalna może ulec zanikowi w czasie ewolucji. Uzyskane wyniki wskazują, że u pszczół istnieje wzór użyłkowania, który jest preferowany przez dobór naturalny. Podobny wzór użyłkowania może się pojawić w wyniku zaniku zarówno pierwszej jak i drugiej żyłki submarginalnej. Utrudnia to ustalenie homologii problematycznej żyłki.

Słowa kluczowe: pszczoły, Apiformes, skrzydło, użyłkowanie, komórki submarginalne, homologia.