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VARIATION OF SEXUAL DIMORPHISM OF THE WING SHAPE IN THE FAMILY DOLICHOPODIDAE (DIPTERA)

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Abstract. Although sexual dimorphism manifestations are widespread in the family Dolichopodidae, a detailed characterization of their phylogenetic significance is lacking. In order to study the distribution patterns of wing sexual dimorphism, we have analyzed 57 species from 17 genera of 9 subfamilies. A comparative analysis of the evidence, obtained by geometric morphometry and molecular data, allowed us to assess the phylogenetic signal in the sexual dimorphism of the wing. The results of the study confirm the presence of diverse patterns of sexual variability in the wings of this family. More often, females have larger wings with blunted apexes, whereas males are characterized by a more pointed apex. In some cases, the larger size of females' wings is associated with an increase in the body size, while in other cases, differences in shape and size can be explained by differences in behavioural and life patterns. Although there exists a general pattern of sexual dimorphism, its features differ even in closely related species. The absence of a significant phylogenetic signal in seven out of nine studied wing points indicates that the sexual dimorphism in form evolved, at least partially, in each of the studied species.

Keywords: Diptera; Dolichopodidae; COI; allometry; geometric morphometry; variability; sexual dimorphism; phylogeny; phylogenetic signal; wing shape; cytochrome c oxidase.

ИЗМЕНЧИВОСТЬ ПОЛОВОГО ДИМОРФИЗМА ФОРМЫ КРЫЛА ДВУКРЫЛЫХ СЕМЕЙСТВА DOLICHOPODIDAE

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Аннотация. Хотя проявления полового диморфизма широко распространены в семействе Dolichopodidae, детальное исследование из филогенетической значимости отсутствует. С целью изучения закономерностей распределения моделей полового диморфизма крыльев, мы проанализировали 57 видов из 17 родов 9 подсемейств семейства. Сравнительный анализ признаков, полученных методами геометрической морфометрии, и молекулярных данных позволил оценить филогенетический сигнал характеристик полового диморфизма крыльев. Результаты исследования подтверждают наличие разнообразных моделей половой изменчивости крыльев в семействе. Чаще всего самки имеют более крупные крылья с притупленной вершиной, тогда как для самцов характерна заострённая форма вершины крыла. В ряде случаев больший размер крыльев самок связан с увеличением размера тела, тогда как в других случаях различия формы и размера могут объясняться различиями в жизненных стратегиях и паттернах поведения самок и самцов. Хотя существует общая картина полового диморфизма формы, однако его особенности различаются даже у близкородственных видов. Отсутствие значимого филогенетического сигнала для семи точек крыла из девяти изученных указывает на то, что половой диморфизм формы эволюционировал, по крайней мере частично, независимо у каждого из изученных видов.

Ключевые слова: Diptera; Dolichopodidae; COI; аллометрия; геометрическая морфометрия; изменчивость; половой диморфизм; филогения; филогенетический сигнал; форма крыла; цитохром-с-оксидаза.

Sexual dimorphism is a phenomenon frequently encountered in the Dolichopodidae family. The most frequent characters of sexual dimorphism are various modifications of tarsi (dense pubescence, distention and protrusion, colour changes), wings (colour changes of the wing membrane, thickened costa), postpedicel elongation and modifications of arista (swelling or protrusion). Such indicators are usually used for diagnostics.

However, more impalpable distinctions between females and males, such as wing shape, are characteristic of the family, and the types of sexual dimorphism of wing shape change from species to species [1, p. 515]. For example, it is found that *Argyra* Macquart, 1834 males perform a mating dance in front of females [2, p. 11], and *Poecilobothrus nobilitatus* (Linnaeus, 1767) males exhibit aggressive demonstrations and chases in rivalry for females [3, p. 602]. Although behavioural traits are considered more evolutionarily labile, they also often carry a significant phylogenetic signal [4, p. 740; 5, p. 7]. In some cases, the wing shape variability can be caused by considerable differences in the body size of females and males, such as in the *Rhaphium appendiculatum* Zetterstedt, 1849.

A wide variety of sexual dimorphism of the wing shape suggests intensive selection. Along with traditional morphological and molecular traits, signs of sexual dimorphism are also a resource for phylogenetic constructions, although such studies are much rare. Thus, a phylogenetic signal in the sexual dimorphism of the wing shape is evident among the *Drosophila* Fallén, 1823 species [6, p. 110]. And what is interesting is the phylogenetic reconstruction of the development of elongated ocelli among males in the family Diopsidae [7, p. 1373].

On the other hand, similar manifestations of sexual dimorphism often occur among non-closely related species. Examples include the formation of an elongated exoskeleton among cheese flies and nereid [8, p. 602], wing spots among fruit flies [9, p. 322], and protrusion and distention on the legs and other body parts among the Diptera of various families [10, p. 143]. Therefore, we can expect that some genetic factors play an essential role in forming a specific pattern of sexual dimorphism, which results in a more pronounced convergence in the morphological characters of nonrelated species than can be explained from a functional point of view.

The analysis of molecular data, together with the sexual dimorphism characters of wing shape, will allow us to consider evolutionary trends of sexual dimorphism, reconstruct ancestral forms, and possibly clarify some controversial points of the phylogenetic tree Dolichopodidae. In the current study, we have analyzed the phylogenetic signal of sexual dimorphism in the wing shape to reveal patterns of distribution between subfamilies and genera.

Materials and methods

In total, 5874 specimens of wing of 57 species of 17 genera belonging to 9 subfamilies were studied (table 1). We used individuals that we collected during 2013–2021 as well as those from the collection of the Department of Ecology and Systematics of Invertebrates, Voronezh State University (Voronezh, Russia).

The analyzed molecular matrix included molecular sequences of the mitochondrial gene encoding cytochrome c oxidase (COI) (810 characters). The study included both sequences previously deposited in GenBank (GenBank, 2021) and sequences carried out especially for this study by the Sintol Enterprise (Russia). In total molecular sequences of 57 species were studied. Amplification and sequencing were performed using the methods and primers described in previous studies [12, p. 455; 14, p. 605]. The sequences were aligned manually using BioEdit multiple alignment software [17]. Phylogenetic reconstruction was carried out using the minimum evolution method (ME) in MEGA software [18]. Reliability of inner branches was estimated by the bootstrap method based on 1000 pseudoreplicates.

Wings were digitized at 9 landmarks (fig. 1). Each landmark has been digitized using TpsDig-2.32 software [19].

For comparing overall wing size among different populations we used the isometric estimator known as centroid size, which is defined as the square root of the sum of the squared distances between the center of the configuration of landmarks and each separate landmark [20, p. 56]. Shape variables were obtained through the Generalized Procrustes Analysis [20, p. 106]. Then, the analysis was carried out using the methods of multivariate statistical analysis in MorpholJ software [21].

The canonical variate analysis was used to determine the most important differences between sexes, and the obtained canonical coefficients for each landmark were used in the further analysis. To construct a dendrogram demonstrating the similarity of patterns of wing shape sexual dimorphism, the unweighted pair group method with arithmetic mean was used. The reliability of internal branching was assessed using bootstrap analysis with 1000 replicas. The statistical significance of pairwise differences in mean shapes of males and females was analyzed using permutation tests (10 000 rounds) with Procrustes distances (PD) [21]. The allometric component of sexual shape dimorphism was estimated by a regression of wing shape on centroid size. Allometric regression lines among females and males were assumed to be parallel. The allometric component of sexual shape dimorphism was the shape change predicted by the size difference between sexes, and the non-allometric component was the difference between this and the total sexual shape dimorphism [6, p. 8].

The phylogenetic signal of wing sexual dimorphism was assessed in two ways. First, the phylogenetic tree (fig. 2) was superimposed on the space of shape variation, and then the hypothesis that the phylogenetic signal was absent was tested using a permutation test with 10 000 integrations. The main components of the shape variability were substituted into the nodes of the phylogenetic tree. The p-value was calculated as the fraction of permutations that lead to the length of the tree, which is equal to or less than that observed for the original data [6, p. 9].

Secondly, as a measure of phylogenetic signal of legs morphometric characters, we used Pagel's lambda (λ) [22] and Blomberg K-statistic [23]. To calculate Pagel's lambda, the *phylosyg* function *phytools* package [24] was used in R environment [24]. Blomberg K-statistic also takes values from zero to one, but if the phylogenetic signal is very high, then K-statistic can rise over one. To calculate Blomberg K-statistic, the *Kkalk* function *picante* package was used in R environment [25]. For testing purpose, the indications of differences of the metric from 0, a p-value was obtained by randomizing the trait data 1000 times.

Table 1 – Studied species

№	Species	Number of specimens		GenBank Accession No. [11]
		males	females	
	Diaphorinae			
1	*Argyra diaphana* (Fabricius, 1775)	22	37	DQ456884.1[a]
2	*Argyra leucocephala* (Meigen, 1824)	15	18	DQ456883.1[a]
3	*Chrysotus cilipes* Meigen, 1824	16	24	DQ456901.1[a]
4	*Chrysotus neglectus* (Wiedemann, 1817)	10	16	DQ456893.1[a]
5	*Chrysotus suavis* Loew, 1857	19	31	DQ456900.1[a]
	Dolichopodinae			
6	*Dolichopus acuticornis* Wiedemann, 1817	14	36	EU847538.1[b]
7	*Dolichopus arbustorum* Stannius, 1831	24	20	OK335810.1*
8	*Dolichopus argyrotarsis* Wahlberg, 1850	34	22	OK335811.1*
9	*Dolichopus austriacus* Parent, 1927	17	9	OK340619.1*
10	*Dolichopus brevipennis* Meigen, 1824	18	17	AY744186.1[c]
11	*Dolichopus campestris* Meigen, 1824	19	39	AY744212.1[c]
12	*Dolichopus cilifemoratus* Macquart, 1827	35	97	AY958243.1[c]
13	*Dolichopus claviger* Stannius, 1831	20	14	AY744206.1[c]
14	*Dolichopus discifer* Stannius, 1831	41	13	AY744208.1[c]
15	*Dolichopus jacutensis* Stackelberg, 1929	5	2	OK336092.1*
16	*Dolichopus kjari* Stackelberg, 1929	7	2	OK340624.1*
17	*Dolichopus latilimbatus* Macquart, 1827	86	77	AY744200.1[b]

№	Species	Number of specimens		GenBank Accession No. [11]
		males	females	
18	*Dolichopus lepidus* Staeger, 1842	48	36	AY744202.1[b]
19	*Dolichopus linearis* Meigen, 1824	19	28	AY958239.1[b]
20	*Dolichopus lineatocornis* Zetterstedt, 1843	24	12	OK340614.1*
21	*Dolichopus longicornis* Stannius, 1831	82	36	AY958240.1[c]
22	*Dolichopus longitarsis* Stannius, 1831	95	110	OK336131.1*
23	*Dolichopus meigeni* Loew, 1857	12	3	OK491386.1*
24	*Dolichopus migrans* Zetterstedt, 1843	36	30	OK446551.1*
25	*Dolichopus nataliae* Stackelberg, 1930	4	3	OK340621.1*
26	*Dolichopus pennatus* Meigen, 1824	41	40	OK446503.1*
27	*Dolichopus plumipes* (Scopoli, 1763)	46	44	EU847548.1[c]
28	*Dolichopus popularis* Wiedemann, 1817	9	19	AY744190.1[c]
29	*Dolichopus remipes* Wahlberg, 1839	13	27	OK446520.1*
30	*Dolichopus ringdahli* Stackelberg, 1930	74	49	OK491385.1*
31	*Dolichopus simplex* Meigen, 1824	41	42	AY744203.1[c]
32	*Dolichopus ungulatus* (Linnaeus, 1758)	201	112	EU847559.1[c]
33	*Ethiromyia chalybea* (Wiedemann, 1817)	16	10	OM572508*
34	*Gymnopternus aerosus* (Fallen, 1823)	76	51	AY744194.1[c]
35	*Gymnopternus celer* (Meigen, 1824)	35	24	EU847565.1[b]
36	*Gymnopternus metallicus* (Stannius, 1831)	102	174	AY744197.1[c]
37	*Hercostomus convergens* (Loew, 1857)	114	143	OK561854.1*
38	*Hercostomus nigriplantis* (Stannius, 1831)	220	125	EU847574.1[b]
39	*Poecilobothrus chrysozygos* (Wiedemann, 1817)	140	37	DQ456948.1[a]
40	*Poecilobothrus regalis* (Meigen, 1824)	450	344	EU847580.1[b]
41	*Sybistroma binodicornis* Stackelberg, 1941	118	44	OL457145.1*
42	*Sybistroma crinipes* Staeger, 1842	43	44	EU847581.1[b]
43	*Sybistroma obscurella* (Fallen, 1823)	30	30	DQ456918.1[a]
	Hydrophorinae			
44	*Hydrophorus borealis* Loew, 1857	10	16	DQ456916.1[a]
45	*Hydrophorus praecox* (Lehmann, 1822)	26	36	DQ456940.1[a]
	Medeterinae			
46	*Medetera jacula* (Fallen, 1823)	8	9	DQ456928.1[a]
47	*Medetera truncorum* Meigen, 1824	10	6	JF716349.1[d]
	Neurigoninae			
48	*Neurigona pallida* (Fallen, 1823)	30	45	HQ449154.1[e]
49	*Neurigona quadrifasciata* (Fabricius, 1781)	16	23	DQ456911.1[a]
	Rhaphiinae			
50	*Rhaphium appendiculatum* Zetterstedt, 1849	36	33	DQ456886.1[a]
51	*Rhaphium commune* (Meigen, 1824)	18	28	DQ456889.1[a]
	Sciapodinae			
52	*Siapus platypterus* (Fabricius, 1805)	18	64	DQ456905.1[a]
53	*Siapus wiedemanni* (Fallen, 1823)	43	44	DQ456950.1[a]
	Sympycninae			
54	*Campsicnemus scambus* (Fallen, 1823)	179	235	DQ456904.1[a]
55	*Syntornom pallipes* (Fabricius, 1794)	31	50	DQ456944.1[a]
56	*Sympycnus pulicarius* (Fallen, 1823)	114	130	DQ456931.1[a]
	Xanthochlorinae			
57	*Xanthochlorus ornatus* (Haliday, 1832)	26	8	HQ449168.1[e]

Note. [a] – [12, p. 468], [b] – [13, p. 243], [c] – [14, p. 604], [d] – [15, p. 665], [e] – [16, p. 314] * – sequences were obtained by the authors of this study.

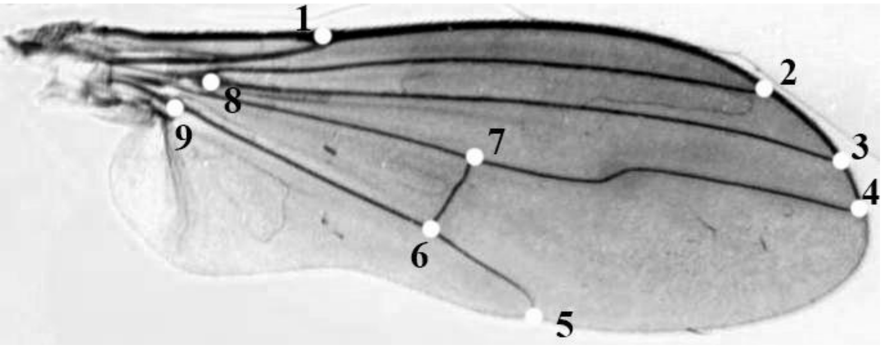

Figure 1 – Wing and landmarks positions

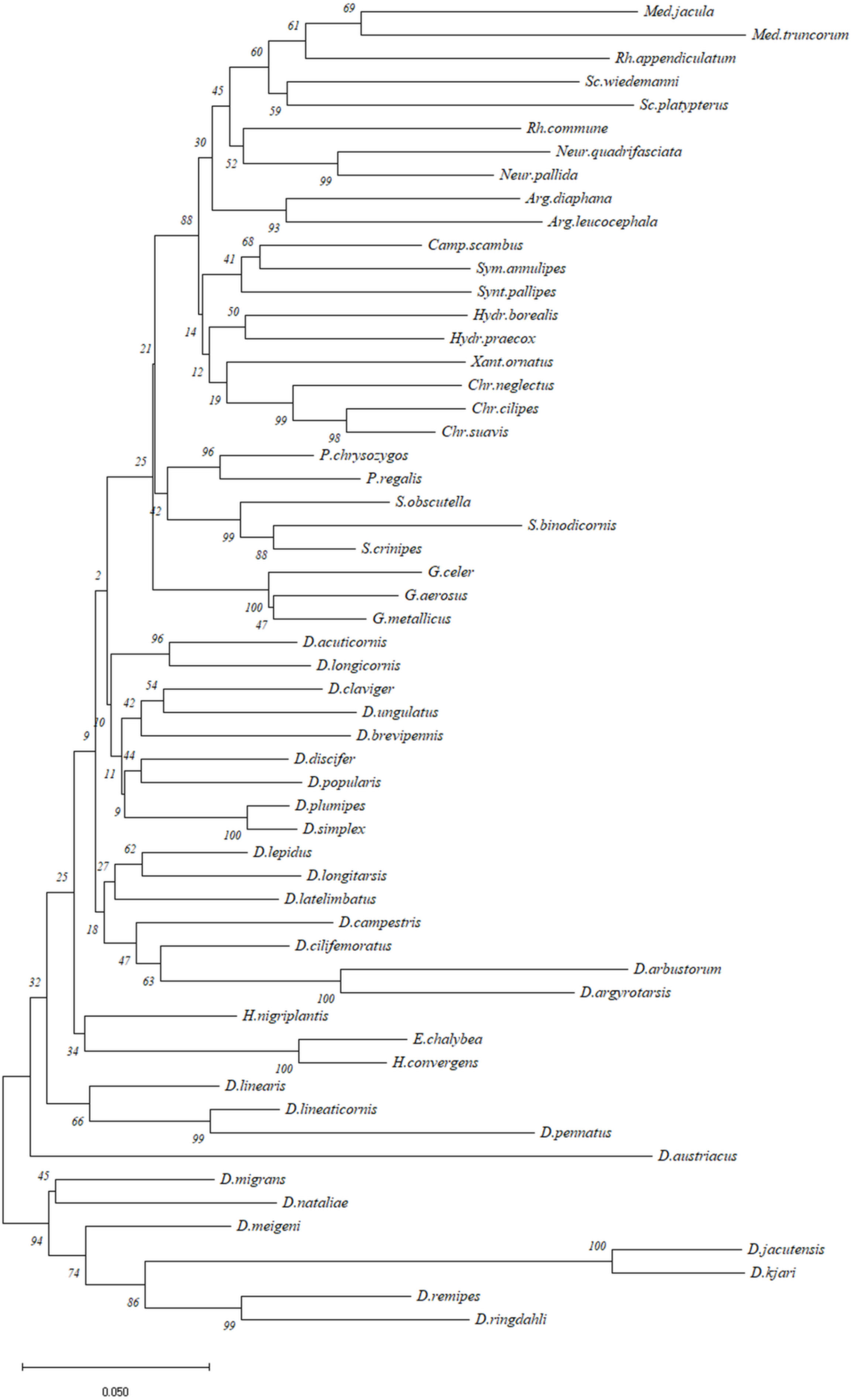

Figure 2 – ME tree, obtained from COI sequences.
Values of bootstrap support from 1000 pseudoreplicates are depicted above nodes

Results

The ANOVA demonstrated that the following factors had a significant effect on sexual dimorphism of wing size: «subfamilies × sex» (F = 3,5; df = 8; P = 0,0005); «genera × sex» (F = 17,5; df = 16; P < 0,0001) and «species × sex» (F = 12,0; df = 56; P < 0,0001). This means that significant differences are observed in the sexual dimorphism of wing size between subfamilies, between genera and between species. Moreover, in 44 cases out of 57, the females wing size exceeded the males wing size. Among the species *Argyra*, *Chrysotus*, *Neurigona*, *Rhaphium*, *Sympycnus*, *Syntormon*, and *Xanthochlorus*, female wings were larger than those of males. Among other species, both situations were encountered.

The smallest sexual difference in size was observed in the species *Campsicnemus scambus*, the largest in the species *Hydr*. *borealis*, *Rh*. *commune* and *Dol*. *argyrotarsus* (female wings are larger than male wings), as well as *Syb*. *crinipes* (male wings are larger than female wings). Among the subfamilies, the largest variation of the difference in wing sizes was characteristic of the Dolichopodinae, the smallest mean value was observed in the subfamilies Medeterinae and Sciapodinae, and the largest in Rhaphiinae.

Differences in sexual dimorphism of wing shape were also significant between subfamilies (Wilks' Lambda = 0,82; F = 20,3; df = 112, 81806,51; P < 0,0001), between genera (Wilks' Lambda = 0,39; F = 51,5; df = 224, 123435,8; P < 0,0001) and between species (Wilks' Lambda = 0,07; F = 42,9; df = 784, 157298,4; P < 0,0001).

The most pronounced sexual dimorphism in the form of a wing was observed among the species *Xanth*. *ornatus* (PD = 0,107; P < 0,0001) and *Arg*. *diaphana* (PD = 0,117; P < 0,0001), the least pronounced among *Gymn*. *aerosus* (PD = 0,006; P < 0,02) and *Herc*. *convergens* (PD = 0,006; P < 0,001). Of the subfamilies, the largest variation in PD values was characteristic of Sympycninae, the smallest average PD value was observed in the subfamilies Medeterinae, Hydrophorinae, and Rhaphiinae, while the largest in Sympycninae and Sciapodinae.

The differences in the sexual dimorphism of wing shape most often consisted in the displacement of Landmarks 3 and 4 along the x-axis, as well as Landmarks 5 along the y-axis, which, in the general case, led to the formation of a more elongated wing with a sharp apex among males and a more rounded wing with a blunt apex – among females.

According to the UPGMA-dendrogram, built on the basis of the canonical coefficients of sexual dimorphism, the most similarity in the sexual dimorphism of the wing shape was shown not always by phylogenetically related species. A similar shape dimorphism has been shown for the following species: *Dol*. *longitarsis* and *Dol*. *ungulatus* (bootstrap index BS = 78), *Dol*. *austriacus* and *Dol*. *lineaticornis* (BS = 50), *Dol*. *acuticornis* and *Gymn*. *aerosus* (BS = 53), *Syb*. *binodicornis* and *Sc*. *platypterus* (BS = 67), *Arg. leucocephala* and *Xanth. ornatus* (BS = 54). The sexual dimorphism of the wing shape of the *Medetera* species was clearly different from the other species of the family (fig. 3).

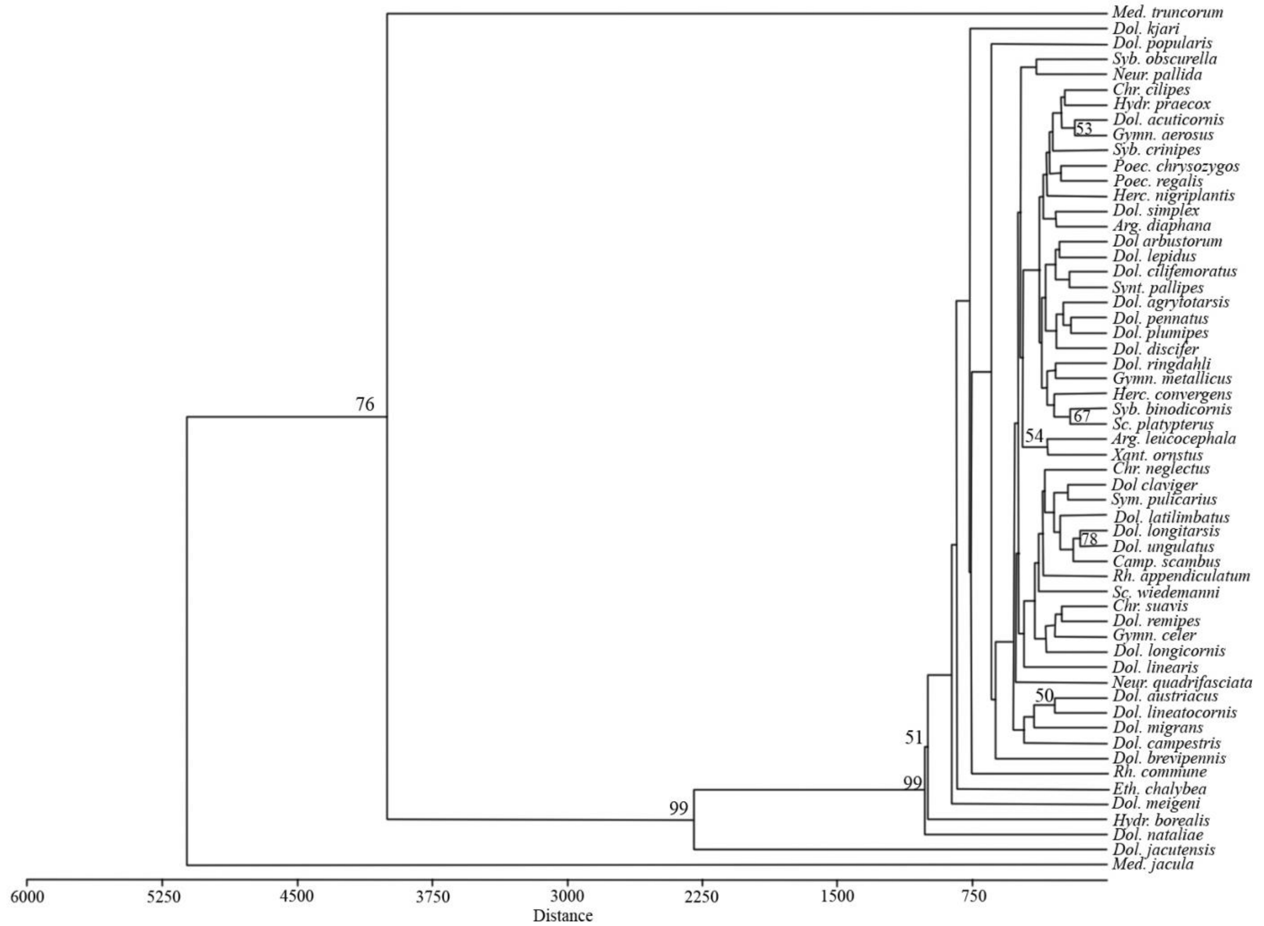

Figure 3 – Results of UPGMA cluster analysis of the canonical coefficients of sexual dimorphism of dolichopodid

It should be noted that the allometric component of sexual dimorphism of the wing shape among most species is expressed insignificantly. The greatest percentage of shape variability associated with the sexual wings size difference was found among the following species: *Syb. obscurella* (40,9%; P < 0,0001), *Dol. meigeni* (37,5%; P < 0,0001), *Dol. austriacus* (34,6%; P < 0,0001), *Dol. kjari* (33,6%; P < 0,0001), *Arg. diaphana* (25,7%; P < 0,0001), *Neur. quadrifasciata* (25,7%; P < 0,0001). The species that showed the largest differences in wing size between females and males did not show a high percentage of allometric variation in shape.

The length of the consensus tree combining the initial molecular data and data on the wing shape changes was 0,1082 (in units of squared Procrustes distance) (fig. 4). The permutation test produced an equal or a longer tree in most cases (P < 0,0001), thus confirming the presence of a phylogenetic signal in interspecific variation of sexual dimorphism in the wing shape.

In the Procrustean distance between the wing shapes of females and males, the minimum phylogenetic signal was observed: $\lambda = 0{,}00007$, P = 1; K = 0,69, P = 0,15. The most significant phylogenetic signal was found for the canonical coefficients of landmarks X1 ($\lambda = 0{,}99$, P = 0,05; K = 1,19, P = 0,003), Y1 ($\lambda = 0{,}99$, P = 0,007; K = 1,31, P = 0,004), Y2 ($\lambda = 0{,}99$, P = 0,02; K = 1,23, P = 0,005).

Discussion

Most of the studied species of Dolichopodidae showed a significant sexual dimorphism of wing shape and/or size, with an insignificant influence of allometry on shape variability. However, the sexual dimorphism of wings in the family is heterogeneous: species of one subfamily showed that the wing size of females exceeds that of males and vice versa; besides, we can distinguish species with significant sexual differences in both wing shape and size (*Arg. diaphana*), species with insignificant sexual differences both in shape and size (*Camp. scambus*), and species with significant differences in wing size and insignificant differences in shape (*Rh. commune*), and also species with slight sexual differences in wing size, but high differences in shape (*Arg. leucocephala*, *Eth. chalybea*). This means that different species are influenced by various selection factors, which may act together or independently on both sexes.

Studies show that female insects are more often larger than males because of the high correlation between body size and fecundity [26]. This may explain that in most cases, the wings of female dolichopodids are larger than those of males since wing size directly correlates with body size. This regularity is well documented among *Rhaphium* species, where differences in body sizes of females and males are maximal. At the same time, sexual dimorphism of wings is shown in differences of size, but not of form (*Rh. commune*), or available differences in form are partially explained by allometry (*Rh. appendiculatum*).

In other cases, when males had larger wing sizes, this could be explained by other factors, e.g., more significant load on males' wings due to different behavioural patterns: fights between males, and peculiarities of mating dance (for example, in *Poec. regalis* males).

Differences in the wing shape of males and females differed in each case but more often consisted in the displacement of 3, 4, and 5 landmarks, i.e., the change in the distal wing part, while the base remains unchanged. The proximal region of the wing is most susceptible to changes, both in the case of sexual, interspecies, and intraspecies variability [1, p. 695].

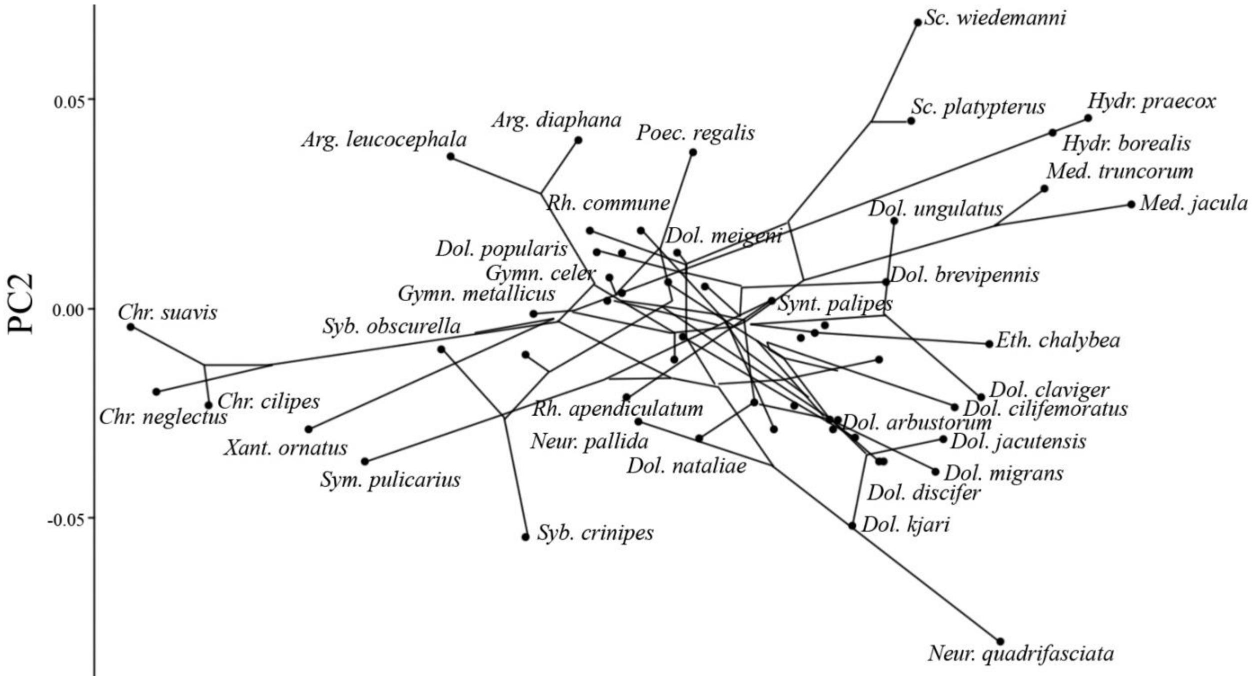

Figure 4 – Changes in the wing shape related to sexual dimorphism mapped onto phylogeny: the first (29,2%) and second (17,8%) principal components of variation

Regardless of the factors influencing sexual dimorphism of wings, our results show that patterns of sexual dimorphism can differ even in closely related species, since even species from different subfamilies turned out to be close in form. This is probably because, in each species, sexual dimorphism of wing shape and size results from complex interactions between several factors of selection that depend on the specific biology, genetic and ecological features, and ontogenetic history of each sex.

Although sexual dimorphism of wing shape appears to be somewhat dependent on common ancestry (the overall phylogenetic signal of sexual dimorphism was reliable), the absence of a significant phylogenetic signal for seven out of nine studied wing points indicates that sexual dimorphism of shape evolved, at least in part, in each studied species.

Conclusion

Our study demonstrates that interspecific differences in the sexual distinction of wing shape in dolichopodids are most often nonallometric and do not depend on phylogenetic relationships between species. These differences are likely the result of a complex interaction of intra-sex competition and other types of selection acting with different intensity in each sex and on several interrelated characteristics, such as body size, wing size, and shape. Overall, the present study results demonstrate that the mechanisms responsible for the emergence of sex differences in wings can form different and complex patterns of sexual dimorphism in the family.

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