Within- and Between-Species Variation of Wing Venation in Genus Monochamus (Coleoptera: Cerambycidae)

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Abstract

We have described the morphological variation of five Western Palaearctic species of Monochamus Dejean, 1821. The variation was assessed using wing measurements. Special emphasis was placed on the differences between Monochamus sartor (F., 1787) and Monochamus urussovii (Fischer-Waldheim, 1805). There was an interesting pattern of variation between the two species. Individuals of M. sartor from the Carpathians differed markedly from individuals of M. urussovii from Siberia, but individuals from north-eastern Poland were intermediate between those two populations. The intermediate individuals were more similar to the Siberian M. urussovii than to the Carpathian M. sartor despite the relatively large geographic distance between north-eastern Poland and Siberia. The occurrence of the intermediate individuals in north-eastern Poland may be the effect of hybridization between M. urussovii and M. sartor, which might have occurred after secondary contact between the two species in the Holocene.

Key words: Cerambycidae, Monochamus, wing, automated species identification, hybrid zone

Genus Monochamus Dejean, 1821 includes about 120 species grouped into 28 subgenera. Most of the species occur in the Holarctic region. In the Western Palaearctic region, there are nine species and in Europe there are five species: Monochamus galloprovincialis (Olivier, 1795), Monochamus saltuarius (Gebler, 1830), Monochamus sartor (F., 1787), Monochamus sutor (L., 1758), and Monochamus urussovii (Fischer-Waldheim, 1805). The biology of the species is relatively well known (Plavilstshikov 1940, Tsherepanov 1983) because they are major pests in forestry (Evans et al. 2004). Monochamus larvae damage bark and cambium and can be fatal to trees. They spread fungi (Jankowiak and Rossa 2007, Jankowiak et al. 2007) and other pathogens of trees including nematode Barsaphelenchus xylophilus (Steiner & Buhrer, 1934) (Nickle et al. 1981, Tóth 2011).

In the western Palaearctic, M. sartor occurs mainly in the Pyrenees, the Alps, and the Carpathian Mountains and rarely in the lowlands (Sláma 1998, Sama 2002). They have been recorded up to an altitude of 1,600 m (Georgiev and Hubenov 2006). The geographic distribution of M. urussovii is relatively large and it ranges from north-eastern Europe (north-eastern Poland, eastern Ukraine, Latvia, Belarus, Scandinavia), through Russia to the Far East (north-eastern China, Korea and Japan) (Plavilstshikov 1940, Tsherepanov 1983, Kolk and Starzyk 1996, Sama 2002, Löbl and Smetana 2010). In Europe, larvae of both M. sartor and M. urussovii feed mainly on spruce but in Siberia M. urussovii also feed on larch, pines, and birch (Tsherepanov 1983, personal observations). Three other Monochamus species: M. galloprovincialis, M. saltuarius, and M. sutor are distributed from the Atlantic Ocean to the Pacific coast (Tsherepanov 1983, Sama 2002, Löbl and Smetana 2010). It is interesting that only in the case of M. galloprovincialis and M. sutor, subspecies were distinguished (M. galloprovincialis galloprovincialis (Olivier, 1795), M. galloprovincialis pistor (Germain, 1818), M. galloprovincialis cinerascens Motschulsky, 1860 and M. sutor sutor (L., 1758), M. sutor longulus Pic, 1898) (Löbl and Smetana 2010). M. galloprovincialis larvae feed mainly on pine but might colonize spruce and larch trees. M. sutor and M. saltuarius feed mainly on spruce but also on fir, pine, and larch (Tsherepanov 1983).

Monochamus species of the western Palaearctic are not very variable. Their identification is based on body size, elytra sculpture, and the presence of hairs on the scutellum (Plavilstshikov 1958, Bense 1995). Two species can be particularly difficult to identify M. sartor and M. urussovii. They are considered sister species after examining morphological (Plavilstshikov 1958) and genetic data (Cesari et al. 2005). Most individuals of the two species can be distinguished by the presence of hairs at the distal part of the elytra. However, in eastern Europe (north-eastern Poland, Belarus, and Lithuania), there are some individuals of Monochamus that have features which are intermediate between the Siberian M. urussovii and European M. sartor. There is some controversy over the taxonomic status of these intermediate individuals. Some entomologists suggest that the intermediate individuals from eastern Europe belong to a subspecies of M. sartor, named as M. sartor urussovii (Sláma 2006, Wallin et al. 2013). According to Sláma (1998) and Danilevsky (2012),
M. urussovii is absent in Poland, the Czech Republic, Slovakia, Ukraine, Belorus, and Lithuania. It was even suggested that individuals identified by Cesari et al. (2005) as M. urussovii were in fact M. sartor (Danilevsky 2012). In this article, we refer to the intermediate individuals as the “Bialowiezan M. urussovii.”

The main aim of this study was to describe the morphological variation between the species and populations of Western Palaearctic Monochamus beetles. The study was based on wing measurements and compared variation in a quantitative way. We verified whether the species differ in wing venation and whether the wing measurements could be used for the identification of species. Furthermore, we compared the morphological differences among European and Siberian populations of M. sutor to the variation between the European and Siberian population of M. urussovii and M. sartor to examine the hypothesis that they are different species or whether they are only populations of a single species. We also used wing measurements to produce a similarity tree and compared it with the results of other studies based on molecular markers (Cesari et al. 2005).

Materials and Methods

Insects

In this study, we used 280 individuals from five species of the genus Monochamus: M. galloprovincialis (24 ♂♂, 24 ♀♀), M. saltuarius (11 ♂♂, 31 ♀♀), M. sartor (21 ♂♂, 22 ♀♀), M. sutor (51 ♂♂, 51 ♀♀), and M. urussovii (31 ♂♂, 14 ♀♀). Specimens were identified using the taxonomic key of Plavilstshikov (1958) and Bense (1995). The material represented five countries, including the eastern part of Russia (Fig. 1). Most of the material was collected during scientific expeditions to the Sajan Mountains, the Baikal, Primorsky Krai, and Tuva regions organized in the years 2012–2014. For more information, see the Supplementary Material. Of particular importance are three populations from which M. sartor and M. urussovii were collected: 1) the Carpathian Mountains (referred to as the Carpathian population), which are located in central Europe on the southern border of Poland, 2) the Bialowieza forest and the Augustow forest (referred to as Bialowiezan population) which is located in central Europe on the border between Poland and Belarus, and 3) Siberia and Far East (referred to as the Siberian population) located in Asia between the river Ob and the Pacific Ocean. The distance between the Carpathian population and the Bialowiezan population is about 400 km, and the distance between Bialowiezan population and the Siberian population is at least 4,000 km. Individuals from the Bialowiezan population were intermediate between the typical forms of M. sartor and M. urussovii. These intermediate individuals were compared individually with typical forms of both species and were classified as species to which they were more similar.

Wing Measurements

The hind wings were used for the measurements (Fig. 2b-f). The wings are membranous, and most of the time they are hidden under the elytra. The wings were detached from the body and mounted on microscopic slides. The mounted wings were scanned with resolution 4,800 dpi using an Epson (Suwa, Japan) V330 Photo scanner. On the wing images, 22 landmarks (Fig. 2a) were determined manually using IdentiFly computer software. Both left and right wings were measured, and the mean value of the two measurements was used in the statistical analysis.

Statistical Analysis

Coordinates of the landmarks were analyzed using tpsRelw software (Rohlf 2014). There was a single orthogonal generalized Procrustes superimposition of all wings to the average configuration. The natural logarithm of the centroid size was used as a measure of wing size and it was analyzed using factorial analysis of variance (ANOVA) in Statistica (StatSoft 2011). Unless specified otherwise, this software package was used in all other statistical analysis. Wing shape was described using partial warp scores, and it was analyzed using multiple analysis of covariance (MANCOVA) with wing size as a covariate. This allowed allometry to be taken into account. To describe

Fig. 1. Collection sites of five species of Monochamus

Fig. 2.
the differences in wing shape between groups, squared Mahalanobis distance (MD) was used. Discrimination between species was based on the canonical variates analysis (CVA) of wings shape. In all cases, leave-one-out cross-validation in PAST software (Hammer et al. 2001) was used to calculate classification rates. The similarity between species was compared using the UPGMA method in PHYLIP software (Felsenstein 2005). The tree was based on squared MDs between species including both males and females. The Białowiezan population of M. sartor and M. urussovi was excluded from the UPGMA.

**Results**

Wing size differed significantly between species (ANOVA: $F(4, 270) = 174.47, P < 0.001$). M. sartor and M. urussovi were larger

![Fig. 2. The hind wings of Western Palearctic species of genus Monochamus; a, landmarks used for the wing measurements; b, M. urussovi; c, M. saltuarius; d, M. sutor; e, M. sartor; f, M. galloprovincialis](image)
than the three other species (Fig. 3). The differences between sexes were relatively small but significant (ANOVA: $F(1, 270) = 6.58$, $P = 0.011$). In all species, females were larger than males and there was no significant interaction between the factors of species and sex (ANOVA: $F(4, 270) = 0.65$, $P = 0.625$). The largest sexual dimorphism occurred in *M. galloprovincialis* and *M. sutor* (Fig. 3).

A MANCOVA revealed that wing shape differed significantly between species but not between males and females (Table 1). The species differed in the allometric relationship as there was significant interaction between factors of species and size. There was also significant interaction between factors of species and sex and interaction between all three factors (Table 1).

CVA showed that the five species of *Monochamus* are distinct (Fig. 4). *M. saltuarius* was particularly well differentiated. On the other hand, there was some overlap between *M. sartor* and *M. urussovii*. The smallest squared MD occurred between *M. sartor* and *M. urussovii* and the largest between *M. sartor* and *M. saltuarius* (Table 2). In pair wise comparisons, all the species differed significantly from each other (Table 2).

CVA allowed species to be identified with relatively high accuracy. The correct classification percentage of all individuals was 95.3% for the “leave-one-out” cross-validation (Table 3). Most of the misclassified individuals were *M. sartor* and *M. urussovii* from Białowieza; therefore, another CVA was carried out in which the Białowiezan populations were treated separately. There were 16 individuals of *M. urussovii* and only one individual of *M. sartor* from this region. The single individual of *M. sartor* was not used for the calculation of canonical coefficients but it was included in the scatter plot of canonical scores. European and Siberian populations of *M. sutor* were also included in this analysis.

The CVA showed that there was a marked difference between the Carpathian *M. sartor* and Siberian *M. urussovii* (squared MD = 27.3). It was more than four times larger than the difference within species between the European and Asian population of *M. sutor* (MD = 6.7, Table 4). In comparison to *M. sutor*, the difference between the Białowieza and Siberian population of *M. urussovii* was two times higher (MD = 13.9, Table 4). On the other hand, the later distance was only slightly smaller than the distance between the Carpathian *M. sartor* and the Białowiezan *M. urussovii* (MD = 18.8, Table 4). The Białowiezan population of *M. urussovii* was intermediate between the Carpathian *M. sartor* and Siberian *M. urussovii* and overlapped both of them (Fig. 5, Table 4).

In pair wise comparisons, the Białowiezan population of *M. urussovii* did not differ significantly from both the Siberian population of this species and the Carpathian population of *M. sartor*; all other populations and species differed significantly from each other (Table 4). The differences between the populations of *M. sartor* and *M. urussovii* were not related to allometry as the populations did not differ in size (ANOVA: $F(2, 84) = 0.83$, $P = 0.439$) and the analysis of residuals of MANCOVA did not markedly change the results presented above.

![Fig. 3. Logarithm of centroid size ± SD of hind wing of five species of Monochamus](image)

![Fig. 4. Differences in wing venation between five species of Monochamus obtained by CVA. First four canonical variates (CV1-CV4) are presented. In the lower graph, only species which were not very well discriminated by the first two canonical variates are shown](image)

### Table 1. MANCOVA of hind wing shape in Monochamus beetles

| Effect            | Wilks $\Lambda$ | $F$  | Effect df | Error df | $P$  |
|-------------------|-----------------|------|-----------|----------|------|
| Sex               | 0.830           | 1.132| 40        | 221.0    | 0.2830|
| Species           | 0.382           | 1.510| 160       | 883.6    | 0.0002|
| Size              | 0.751           | 1.834| 40        | 221.0    | 0.0033|
| Sex*species       | 0.441           | 1.261| 160       | 883.6    | 0.0235|
| Sex*size          | 0.825           | 1.169| 40        | 221.0    | 0.2393|
| Species*size      | 0.376           | 1.536| 160       | 883.6    | $<0.0001$|
| Sex*species*size  | 0.441           | 1.239| 160       | 883.6    | 0.0243|
The UPGMA similarity tree (Fig. 6) confirmed that *M. sartor* and *M. urussovii* are very similar to each other in terms of wing venation. There was increasing distance from this pair of species to *M. galloprovincialis* and *M. sutor*. *M. saltuarius* differed most from all other species (Fig. 6).

### Discussion

The data presented here show that the measurements of wing venation are helpful to distinguish between five species of *Monochamus*. The semi-automated measurements can be useful not only for non-specialists but also for experienced entomologists because the identification of some *Monochamus* species can be difficult. This is particularly

### Table 2. Squared MDs between five species of *Monochamus* (top right triangle) and significance of pair wise differences between the species (bottom left triangle)

|                  | *M. sutor* | *M. urussovii* | *M. saltuarius* | *M. sartor* | *M. galloprovincialis* |
|------------------|------------|----------------|-----------------|-------------|------------------------|
| *M. sutor*       | —          | 42.85          | 74.31           | 56.31       | 40.39                  |
| *M. urussovii*   | ***        | —              | 87.69           | 14.68       | 25.35                  |
| *M. saltuarius*  | ***        | ***            | —               | 89.99       | 62.05                  |
| *M. sartor*      | ***        | ***            | ***             | —           | 24.49                  |
| *M. galloprovincialis* | ***        | ***            | ***             | ***         | —                      |

**p** value lower than 0.0001.

### Table 3. Classification of *Monochamus* species based on wing venation

| Species          | Correctly classified (%) | Classified as |
|------------------|--------------------------|---------------|
|                  | *M. galloprovincialis*   | *M. saltuarius* | *M. sartor* | *M. sutor* | *M. urussovii* |
| *M. galloprovincialis* | 94                      | 45            | 0           | 2          | 0          |
| *M. saltuarius*   | 100                      | 0             | 42          | 0          | 0          |
| *M. sartor*       | 91                       | 0             | 0           | 39         | 0          |
| *M. sutor*        | 99                       | 1             | 0           | 0          | 101        |
| *M. urussovii*    | 89                       | 0             | 0           | 5          | 0          |

### Table 4. Squared MDs between population of *M. sartor*, *M. sutor*, and *M. urussovii* (top right triangle) and significance of pair wise differences between the populations (bottom left triangle)

|                  | *M. urussovii* (Siberia) | *M. urussovii* (Bialowieza) | *M. sartor* (Carpathians) | *M. sutor* (Europe) | *M. sutor* (Siberia) |
|------------------|--------------------------|-----------------------------|---------------------------|---------------------|----------------------|
| *M. urussovii* (Siberia) | —                        | 13.97                       | 27.31                     | 49.87               | 56.80                |
| *M. urussovii* (Bialowieza) | NS                      | —                           | 18.86                     | 56.57               | 63.74                |
| *M. sartor* (Carpathians) | ***                     | NS                          | —                         | 70.07               | 83.03                |
| *M. sutor* (Europe)    | ***                      | ***                         | ***                       | —                   | 6.75                 |
| *M. sutor* (Siberia)   | ***                      | ***                         | ***                       | ***                 | —                    |

NS, nonsignificant.

**p** value lower than 0.0001.

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**Fig. 5.** Differences in wing venation between populations of *M. sartor*, *M. sutor*, and *M. urussovii* obtained by CVA

**Fig. 6.** UPGMA tree of five species of *Monochamus* based on the wing venation
true in the case of some specimens of M. sartor and M. urussovii. There is an interesting pattern of variation between the two species. The difference between the Carpathian M. sartor and the Białowieża M. urussovii is similar to the difference between the Białowieża M. urussovii and Siberian M. urussovii despite the fact that the distance between Białowieża and Siberia is more than 10 times larger than the distance between the Białowieża and the Carpathians. For comparison, the difference between the European and Siberian population of M. sartor is much smaller (Fig. 3, Table 4).

This pattern of variation can indicate the presence of hybrid zones between M. sartor and M. urussovii. The two species are considered to be vicariant (Hellrıglı 1971). It is possible that during Pleistocene glaciations M. sartor persisted in European refugia and M. urussovii in Siberian refugia. The hybrid zone could have been formed after secondary contact between the two species in the Holocene when spruce forests extended their distributions into central and northern Europe. To verify if the secondary hybrid zone is present, more samples of M. sartor and M. urussovii should be collected along a transect between the Carpathian Mountains and Scandinavia. If a hybrid zone is present, there should be coinciding clines of variation for various morphological and genetic traits (Szymura 1993). The stability of the hybrid zone between M. sartor and M. urussovii can be affected by the disjunctive distribution of spruce which is the main food plant (at least in Europe) for both M. sartor and M. urussovii. One of the gaps in the spruce distribution range occurs between populations in central Europe and north-eastern Europe (Boratyński 2007). Picea abies from the Alpine-Carpathian refuge occurs in the south of Poland, and Scandinavian-Siberian spruce is present in the north-east region (Zajac and Zajac 2001). The two populations differ both morphologically and genetically (Modrziński and Prus-Głowacki 1998).

Some researchers suggested that the Białowieża M. urussovii is in fact M. sartor (Śląma 1998, Śląma 2006, Danilevsky 2012, Wallin et al. 2013). However, in terms of wing venation, this population is more similar to the Siberian M. urussovii than to the Carpathian M. sartor (Table 4). On the other hand, the population differs markedly from the Siberian M. urussovii; therefore, the taxonomic status of the intermediate individuals remains unclear. If there is a gene flow between M. sartor and M. urussovii, it can be argued that the two species should be synonymized. However, the difference in wing venation between the Carpathian M. sartor and Siberian M. urussovii is larger than the difference between other species in the same genus, for example, between M. galloprovincialis and M. urussovii (Tables 2 and 4). Therefore, it seems to be more consistent to classify the two populations as species and not subspecies. Distinction between the two taxonomic levels is not clear and depends on the definition of species. If concept of biological species is applied than the viability of hybrids between M. sartor and M. urussovii should be compared with the viability of typical individuals of the two species.

It is possible that part of the geographical variation of Monochamus beetles is related to environmental factors. It is known that insect wings can be affected by diet (Shingleton et al. 2005, Berns 2014), altitude (Pitchers et al. 2013) and developmental temperature (Debat et al. 2003). In the case of Monochamus, the influence of diet is possible because one species of beetle can feed on many tree species. In Europe, M. urussovii feeds only on spruce, but in Siberia, it might colonize also larch, fir, pines, or even birch. It is unknown if M. urussovii developing in different tree species differ morphologically; however, it is unlikely that the effect of diet is large because the Siberian M. urussovii, which feeds on many species of trees, is no more variable than the Białowieża M. urussovii which feeds only on spruce (Fig. 5).

The similarity tree produced using the wing measurements resembles the combined tree produced using molecular methods (Fig. 1d in Cesari et al. 2005). In particular, M. sartor and M. urussovii are very similar to each other and M. saltinusius differs most from all other species. However, in the tree presented here, M. galloprovincialis and M. sutor are not sister species as in the other study (Cesari et al. 2005). It is often suggested that wing measurements are not suitable for the reconstruction of phylogeny because wing shape is under strong selection and it reflects adaptation to environment more than phylogenetic history. Consequently, phylogenetic signals in morphometric data are diluted by processes leading to homoplasy, such as reversals, parallel evolution, and convergence (Klingenberg and Gidaszewski 2010). However, in some studies, there was an agreement between wing morphology and phylogeny (Bai et al. 2011, Perrard et al. 2014). The suitability of wing measurements for the reconstruction of phylogeny can depend on the selective importance of flight. In comparison to other insects, beetles do not fly very often. There are several genera with completely reduced hind wings among families with predominantly flying beetles (Frantsevich et al. 2015). In this situation, it is possible that the variation of wing venation in beetles is not adaptive. Therefore, in this group, wing measurements can be a useful method of investigating phylogeny.

The data presented here confirm that intra- and interspecies variation can be described quantitatively using wing measurements. The morphological similarity between species based on measurements agrees to a large degree with published earlier phylogeny. The measurements allowed the semiautomated identification of five Western Palaearctic Monochamus species with over 95% accuracy and can be easy to use even for nonspecialists. The fast and correct identification of this group is particularly important because Monochamus beetles are considered to be major pests. Earlier studies were focused on the qualitative traits of controversial individuals of M. urussovii from Białowieża. Here, we have used quantitative traits and samples from various geographic locations to show that Białowieża M. urussovii are more similar morphologically to the typical Siberian M. urussovii than to the Carpathian M. sartor. This is a very interesting result, especially with regards to the views of some researchers, that M. urussovii is absent in Eastern Europe (Danilevsky 2012). On the other hand, the Białowieża M. urussovii is also quite similar morphologically to the Carpathian M. sartor. We suspect that this pattern indicates the presence of a hybrid zone, though more research is required to confirm this.

**Supplementary Data**

Supplementary data are available at Journal of Insect Science online.

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