INFRASPECIFIC TAXONOMY OF SYMPETRUM PEDEMONTANUM (MÜLLER, 1766)* (ANISOPTERA: LIBELLULIDAE)

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An analysis of a large series of specimens from Eurasia showed a strong morphological variability. It is of an individual, modificatory, or clinal nature, rather than a geographical one. Thus, 2 continental sspp., *S. p. intermedium* Belyshev, 1955 and *S. p. kurentzovi* Belyshev, 1956, should be suppressed as they cannot be defined by any taxonomically significant differences. The insular subspecies, *S. p. elatum*, inhabiting Sakhalin, the Kurile and the Japanese islands, however, can be separated. It is concluded that *S. pedemontanum* has only 2 sspp.: continental *S. p. pedemontanum* and the insular *S. p. elatum*.

INTRODUCTION

The distribution of *Sympetrum pedemontanum* extends from the Pyrenees to the Kuril Islands in the middle belt of Eurasia (Fig.1). It occupies the area unevenly and forms local concentrations associated with foothill zones. It is interesting to consider two peculiarities of this species. Firstly, it has stable high numbers in some concentrated popu-

* There is some controversy as to the authorship of *S. pedemontanum*. I have examined the original publication and, in brief, the matter is as follows. During his trip to Torino (Italy), Otto Friedrich Müller did some insect collecting there, and subsequently prepared a report, which he sent to Carlo Allioni, who was a helpful host during his visit. In this report Müller listed 8 odonate species, including a new one, which he described and named as *Libellula pedemontana*. Allioni edited the text and published the paper in the *Mélanges de Philosophie et de Mathématique de la Societé royale de Tourin*, in the volume for 1762-1763, that appeared in 1766. The article was titled "Manipulus insectorum taurinensium, a Carlo Allioni editus". In the Preface, p. 185, he clearly stated that "Manipulus hic insectorum pertinet ad C. virum Ottonem Fridericum Müller". The author of *S. pedemontanum* is, therefore, O.F. MULLER (1766). Since, typographically, the name of Allioni appears in the title, while that of Müller occurs only in lines 1-2 in the text, the authorship was erroneously ascribed to Allioni. HAGEN (1862) was the first to draw the attention to this fact, but his statement remained unnoticed or neglected. Recently, d'AGUILAR (2000) again arrived to the same conclusion. lations, while in most habitats it occurs sporadically. Secondly, bright wing coloration (the presence of a brown band) is not typical of temperate latitude dragonflies.

It is generally considered that Sympetrum pedemontanum consists of four subspecies (BELYSHEV et al., 1989; BRIDGES, 1993; DAVIES & TOBIN, 1985; TSUDA, 2000): S. p. pedemontanum (Müller, 1766) (from the western extremity of the area as far as the Altai; Fig. 1p), S. p. intermedium Belyshev, 1955 (from the Altai to the Middle Amur; Fig. 1i), S. p. kurentzovi Belyshev, 1956 (from the Middle Amur to the Pacific Ocean; Fig. 1k) and S. p. elatum (Selvs, 1872) (Sakhalin, the Kurile and the Japanese islands). Among these only S. p. elatum is insular. It has the following taxonomical biography. In 1872 Selys-Longchamps recorded Diplax pedemontana from Japan, and in 1884 defined it as Diplax pedemontana race elata. Most authors accept the subspecific rank of the Japanese population (e.g. YAKOBSON & BIANKI, 1905; RIS, 1911; BE-LYSHEV, 1956, 1973; ASAHINA, 1961; DAVIES & TOBIN, 1985; TSUDA, 2000; WATANABE & TAGUCHI, 1988; BELYSHEV et al., 1989; MALIKOVA, 1995), some other consider it as a separate species, S. elatum (KIRBY, 1890; BARTENEV, 1915). The structure of the male genitalia and the anal appendages of S. pedemontanum from continental and insular parts of its range have been analysed. The structure of the genitalia is practically invariable, whereas in the structure of the anal appendages there are differences which can be regarded as subspecific. I believe, therefore, that elatum is the insular subspecies of S. pedemontanum, rather than an independent species. The clarification of the taxonomic status of the continental subspecies, intermedium and kurentzovi, is the main subject of the present paper.

We collected large series from the northern Caucasus (ca 300 specimens) and we examined ca 200 specimens from the collections of the Institute of Animal Systematics and Ecology (Siberian Branch, Novosibirsk, Russia). Thus, large material from differ



Fig. 1. Sympetrum pedemontanum, ranges of the named infraspecific taxa: $\square - S$. p. pedemontanum (p: S. p. pedemontanum, - i: S. p. intermedium, - k: S. p. kurentzovi); $\square - S$. p. elatum.

ent parts of the range (N Caucasus, SW Siberia, Middle Asia, and the Russian Far East Primorye) was analyzed. It was found that the species is extremely variable. Almost every morphological parameter used has a definite amplitude of variability; and in practically every part of the area, with rare exceptions, all versions of each phenotype (with various frequencies of occurrence), exist. There is strong variability in coloration and dimensions of the specimens, in wing venation, and in intensity of coloration, width, shape and position of the wing band.

MATERIAL AND METHODS

About 500 specimens of *S. pedemontanum* from the main parts of its range (N Caucasus, SW Siberia, Middle Asia and Primorye) were examined. Such morphological parameters as coloration and dimensions of body, wing venation, coloration intensity, width, shape and position of the wing band were studied to ana-



Fig. 2. Sympetrum pedemontanum: colour variability in males (head, legs; in %).

lyse the variability of the species. The quantitative and qualitative data were treated by two methods: standard variation statistics and the main components method.

RESULTS AND DISCUSSION

The basic colour of the body changes from yellow to red. As a rule the latter is more often found in adult individuals. BELYSHEV (1956: p. 185) remarked that only Primorye specimens of adult males have a reddish labrum and frons. According to our data, the face of all adult males is of lemon, brown or red colour, and shades of these, in all populations investigated. In Primorye populations, the percentage of the specimens with red faces turned out only a little higher than in other ones (Fig. 2).

An analysis of all the material was carried out to check for the presence or absence of the black pattern in the different parts of the body. In this case, a 2, 3 or 4 point estimation scale was used to reflect the degree of black coloration present on the insect's body



Fig. 3. Sympetrum pedemontanum: colour variability in males (thorax, abdomen; in %).



Fig. 4. Sympetrum pedemontanum, variability of some features in populations from different parts of its range: (a) North Caucasus ($n = 160 \delta$, 140 \Im); - (b) SW Siberia ($n = 30 \delta$, 32 \Im); - Middle Asia ($n = 35 \delta$, 30 \Im); - (d) Primorye ($n = 38 \delta$, 35 \Im). - [Vertical lines: variability amplitude; - horizontal lines: mean value; - shaded rectangle: s.d. either side of the mean; - unshaded rectangle: 2 s.e. either side of the mean]

(Figs 2, 3). As a result we have a motley mosaic of different dimensions and shades of black spots in which no definite trend in the characters could be traced. Only a weak tendency for a greater development of black coloration in the eastern specimens was recorded. On the whole, all colour variants are within the bounds of individual or age variability.

The abdominal length and hind wing length were used. The diagrams (lower) in Figure 4 show the variability limits of these parameters in populations from the continental part of the area. A strong overlapping of both the abdominal length and hind wing length in the samples from different populations is apparent, while statistically reliable differences do not exist.

It is also interesting to note that a correlation between dragonfly dimensions and wing band width was not found. To be precise, a true positive correlation was discovered in 7 out of 20 cases (in two populations only for males and in one population both for males and females); true negative correlation was discovered only in one case (for males); in the remaining 12 cases, there was no linear correlation. Thus, the correlations between these three parameters occur sporadically and do not appear to be significant.

For the first time the wing venation of *S. pede-montanum* was studied in detail: the number of cells in 11 different zones was counted and statistically analysed for each wing from different populations. The results were as follows:

- The smaller the calculated cell zone the greater is the degree of variability;
- The least variable appear the costal and subcostal fields;
- (3) The differences between the left and right wing venation, in both fore and hind wing, are insignificant, the venation is effectively symmetrical;



Fig. 5. Sympetrum pedemontanum, Middle Asia: variability in shape and location of wing band.

- (4) The true differences were revealed in the venation of the same zones in the fore and hind wings;
- (5) The variability in venation within each of the populations investigated is rather high;
- (6) The variation in wing venation within populations of any region is comparable with the variation between the populations from different regions.

The most variable feature appears the wing band with all its parameters. In each population its shape and position are very different. This makes it very difficult to reveal any pattern. This variability is clearly shown in the populations from Middle Asia (Fig. 5). The colour of the band is brown but of different shades. To make it easier to analyse, the colour intensity was evaluated on a 3-level estimation scale, i.e. pale, middle and bright (strongly coloured) (Fig.6). The data were unexpected: the band in both young and adult individuals of both sexes could be pale, middle or bright. However, it has been generally accepted that the colour intensity of the band definitely increases with age. A bright band in young dragonflies is more an exception than a rule. Nevertheless, on the whole, a strong correlation between age and band colour intensity was not revealed. It is worth mentioning that the band in freshly emerged *S. pedemontanum* is scarcely visible. Besides, within each investigated population practically all the variants of the estimation scale are present and only pale specimens are absent sometimes. The highest percentage of bright-banded specimens occurs in the farthest extremes of the area, i.e. in the populations of the North Caucasus and Primorye.



The most variable feature of S. pedemontanum is the band width (measured alongside the radial sector Rs). According to BARTENEV (1915, p. 142) it varies from 3.5 to 6.0 mm; according to Ris (see BARTENEV, 1915) 2.0-4.0 mm in Swiss specimens. According to our data, using material from the whole area of species distribution, the band width varies from 2.5 to 6.7 mm (Fig. 4, upper diagram). In the hindwings the band is usually a bit wider than in the forewings. Sometimes they are of equal size. There are sex differences: usually the band of both wing pairs is wider in males than it is in females. Interesting examples occur in each separate region. For instance, we investigated two populations in the North Caucasus (Kabardino-Balkaryan Republic). These are Mayskaya, i.e. low country population and Priel'brusskaya, i.e. mountain one (Fig. 7). The wing pigmentation of low country specimens is more developed than that of mountain ones. For females, the means differed by more than the sum of their standard deviations (for each population) on the fore or on the hind wings. We saw the same in mountainous populations in Tajikistan (Garm), where the band width is not just narrower than in other regional populations, but it has almost disappeared in some specimens, its traces remaining only in the region of the pterostigma. Probably in the North Caucasus and Tajikistan



Fig. 7. Sympetrum pedemontanum, North Caucasus, variability of wing band: (a) lowlands; - (b) highlands. - [Vertical lines: variability amplitude; - horizontal lines: mean value; - shaded rectangle: s.d. either side of the mean; - unshaded rectangle: 2 s.e. either side of the mean].

we come across a modified variability of the character, which is caused by certain ecological conditions. Having compared the populations of different regions, we got a continuous gradient with a tendency to the band widening when moving through the area from West to East. So we can speak of clinal variability on the basis of this feature, especially as other clines are found for almost all continental animal species (MAYER, 1968, p. 291).

To compare the samples from different parts of the species' range we simultaneously used two methods: standard variation statistics (see above) and the main components method. 14 quantitative and 8 qualitative features of the samples (in 15 specimens) from Primorye, West Siberia, Middle Asia and the North Caucasus were measured. The qualitative features were transformed into dichotomous ones. There were 30 features in total. The averages of all features were treated by the main components method (Fig. 8). The analysis of variability by this method confirms the absence of taxonomically substantial differences among diverse continental geographic populations.



Fig. 8. Location of Sympetrum pedemontanum samples from four geographical populations in the plane of the second and third main components, calculated by 30 features: $\boxtimes N$ Caucasus; $- \blacktriangle$ SW Siberia; $- \times$ Middle Asia; $- \blacksquare$ Primorye.

CONCLUSION

All samples from continental populations have very variable morphology and no statistically reliable differences exist. In each case examined, the nature of the variability is different. It is individual, modificatory, or clinal in nature and not geographical. Consequently, all mainland subspecies (with the exception of the nominate) should be suppressed as they exhibit no taxonomically significant differences. On the basis of all qualitative characteristics, however, the insular subspecies *S. p. elatum* inhabiting Sakhalin, Kuril and the Japanese islands (POPOVA, 1998), may be separated from the nominate subspecies. Thus, *Sympetrum pedemontanum* has only two infraspecific taxa: the continental *S. p. pedemontanum* and the insular *S. p. elatum*.

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