

**BREAKING THE *CALOPTERYX*-BOTTLENECK: TAXONOMY AND RANGE OF *CALOPTERYX SPLENDENS WATERSTONI* SCHNEIDER, 1984 AND OF *C.SPLENDENS TSCHALDIRICA* BARTENEV, 1909 (ZYGOPTERA: CALOPTERYGIDAE)**

H.J. DUMONT<sup>1</sup>, A. DEMIRSOY<sup>2</sup> and D. VERSCHUREN<sup>1</sup>

<sup>1</sup>Institute of Ecology, State University of Ghent, Ledeganckstraat 35,  
B-9000 Gent, Belgium

<sup>2</sup>Biology Department, Hacettepe University, Beytepe-Ankara, Turkey

*Received and Accepted February 25, 1987*

The range of *C. s. waterstoni* is defined. It is bounded to the west by *C.s. amasina*, with which it hybridizes in a river valley at Görele. The wide variability of the hybrids indicates that they themselves are fertile, and therefore establishes the subspecific level of both taxa. It is suggested that the eastern boundary of ssp. *waterstoni* is defined by hybrid population(s) (*C. s. waterstoni* x *C. s. mingrelica*) north of Batum, originally identified as *C. s. tschaldirica* by Bartenev. The south-western range boundary of the latter taxon, which is shown to be valid, is also redefined. It is confined to some high plateaus of Eastern Anatolia and the S.S.R. Armenia, is broadly separated from *C. s. waterstoni* by the valley of the middle and lower Çoruh River in the west, and hybridizes with *C. s. amasina* in the South along a fairly wide area of intergradation. — The present study bears heavily on the general taxonomic situation within *C. splendens*. In redefining the components of this complex, as much weight should be given to range boundaries as to morphology.

## INTRODUCTION

The taxonomy of the *Calopteryx splendens*-group, a supra-specific complex extending over most of the palaearctic, has been a matter of controversy for more than a century. None of its constituent taxa can be differentiated by structural characters, and females are almost impossible to tell apart. Reproductive isolation is believed to be achieved by ethological rather than by morphological barriers, and male courtship display is the key to it (BUCHHOLTZ, 1955; HEYMER, 1977).

Courtship display involves a male dance, accompanied by extensive wing

clapping. Associated with this is the shape and size of four coloured wing spots which, though not limited to males, are much more frequent in this sex. Moreover, where homochrome females are found, they are usually limited to some of the better defined subspecies.

The extremes between which a male wing spot may vary is total absence (a condition found in the North-African *C. exul*, and in two different races of *C. splendens*), and total coverage of the wing. The latter condition is only found in some races of *C. virgo*, but a wing spot extending between the wing tip and all but its very base occurs in at least two or three races of *C. splendens*. While most taxonomists agree that a "wing-spot based" subdivision of *C. splendens* s.l. is a natural one, the apparent or real intrapopulation and interpopulation variation of this character still leads to much frustration and dissatisfaction. Although *C. splendens* is a typical running-water damselfly with limited capacity for dispersal, it is unthinkable that no gene flow at all would occur between adjacent populations. Because of the slow pace of such a gene flow, especially in mountainous areas where individual river basins may be regarded as island ecosystems, one might a priori expect adjacent populations to build clines. In fact, the steepness of such clines should be a direct measure of the physical isolation of a given taxon.

Anatolia (Asian Turkey) provides a classic example of a mosaic of isolates inhabited by different subspecies of one "master" species, not only in dragonflies but in many other biota as well (DEMIRSOY, 1979). The most recent review of the taxonomy of *C. splendens* in this country is given by DUMONT (1977), but is definitely an oversimplification and therefore obsolete. SCHNEIDER (1984) described *Calopteryx waterstoni* from the eastern Black Sea coast of Anatolia, based on few specimens from a single locality. It is obviously a member of the *C. splendens* group, distinctive by the total absence of a coloured wing spot in the male. Further south-east, from the high plateaus of the S.S.R. Armenia and Eastern Anatolia, BARTENEV (1909) had described another taxon, *C. s. tschaldirica*, characterized by male wings with a small, circular spot, not connected to the wing margins.

It occurred to us that the nearness of the ranges of both taxa, and the gradation from a totally absent, through a small, to an extensive (*C. s. amasina*-like) wing spot might provide a possibility to test the hypothesis of cline formation between subspecies of *C. splendens*. Consequently, two surveys of the Pontic Alps were set up, in June-July 1985, and July 1986, respectively.

### THE RANGE OF *Calopteryx splendens waterstoni*

Moving east along the Black Sea coast from Samsun onwards, successive rivers drain towards the sea in a parallel fashion, each system being isolated from the next. Dragonflies were collected at regular intervals, with special attention to *Calopteryx*. Between the site of Görele in the west and Kemalpaşa near the Russian border in the east (Fig. 1), eight populations of *C. s. waterstoni* were discovered. We do not know for certain whether the easternmost population

corresponds to the true eastern limit of extension of the taxon, but we were able to ascertain that the middle valley of the Çoruh River, which originates in Turkey but is the westernmost major river flowing into the Black Sea in the USSR, is empty of *Calopteryx splendens* forms. This sets a south-eastern boundary to the subspecies' range. Only slightly north-east of the Çoruh mouth, BARTENEFF (1930) found a population which he ascribed to *Calopteryx s. tschaldirica* (Fig. 1). We shall return to the nature of this population later.

*Calopteryx s. waterstoni* is also strictly confined to the low-altitude coastal zone of the Black Sea. No populations were found at altitudes of more than a few hundred meters above sea level. Its overall range is therefore small and neatly circumscribed: the Pontic alps in the south, the lower Çoruh in the north-east, the Görele river in the west (Fig. 1).

#### THE HYBRID POPULATION AT GÖRELE

A population inhabiting a river valley near Görele was discovered along the road to Çanakçı, about 17 kilometers inland. The nearest population of *C. s. waterstoni* occurs at Eynesil, about 12 kilometers to the east. The nearest colony of *C. splendens*, which we tentatively ascribe to *C. s. amasina* (BARTENEFF, 1912), was found about 20 kilometers to the west, on a river near Esbiye.

Out of 39 males collected at Görele, 15 possess hyaline wings and look like pure *C. s. waterstoni*. In only one male a wing spot comparable in size to that of *C. splendens* from Esbiye occurs. The remaining 23 specimens represent transitional forms, with wing spots of

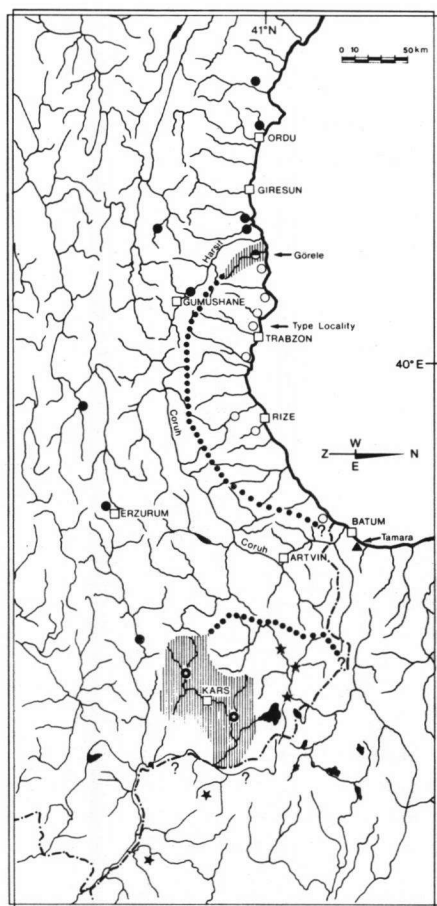


Fig. 1. *Calopteryx splendens* ssp. in NE Turkey and the adjacent USSR. (Open circles: *C. s. waterstoni*; — Closed circles: *C. s. amasina*; — Stars: *C. s. tschaldirica*; — Triangle: record of *C. splendens* ssp. by BARTENEFF, (1930); — Dotted line: range boundary; — Hatched: transition zones).

variable sizes. They could — somewhat arbitrarily — be assigned to six categories, with wing spots ranging from almost complete to hardly visible (Fig. 2). Whether these categories represent distinct genotypes is beyond our present insight. However, if we accept the hypothesis that crossings between the two pure subspecies produce half-way intermediate hybrids, the wide variability encountered can only be explained by the ability of these hybrids to reproduce successfully themselves. Hybrids were actually seen in tandem formation, and we can assume that they not only mate, but are also fertile.

If females of ssp. *waterstoni* indulge in copulation with males of ssp. *amasina*, or vice versa, this means that shape and size of the male wing spot is not carrying great weight in the overall male courtship display of these two races. Actually, when on the wing, males of *C. s. waterstoni* look almost as brilliant as their cousins with coloured wings.

The metallic blue of *Calopteryx* males is caused by light scattering in the cells of the epidermis, which contain randomly dispersed colourless granules and a layer of dark brownish-violet ommatin pigment at their base (FOX & VEVERS, 1960). The blue metallic colours arise when light is scattered by the colourless granules which act as optical heterogeneities. Because this scattering is easily masked by reflected white light, a background of absorbing material, such as ommatin (formerly confused with melanin) is necessary (FOX, 1953). In male *C. s. waterstoni*, light scattering, producing blue metallic sheens, is confined to the wing veins, but is by no means absent. Courting males, with vibrating wings, produce the illusion of having light-blue coloured wings.

The detailed ecological requirements of the hybridizing races remain to be studied. However, it seems that *C. s. waterstoni* (see further) is competitively superior to *C. s. amasina* in cold-water rivers only, and is prevented by the latter from colonizing all other biotopes. Further, it remains to be shown whether females of *C. s. amasina* actually accept to mate with males of *C. s. waterstoni*. The evidence at hand, and especially the frequency of the different male wing spot phenotypes, argues for Görele as a boundary population of ssp. *waterstoni*, occasionally invaded by wandering specimens of ssp. *amasina*. At least part of the latter (one sex? both sexes?) succeed in mating with *C. s. waterstoni*, giving rise to fertile hybrids. As a consequence, the taxon *waterstoni* must be classified as a subspecies of *C. splendens*. It is not a good species, in spite of its distinctive habitus.

Hybrids crossing with true *C. s. waterstoni* generate a gradual dilution of the, evidently polygenic, wing spot character. The long-term evolution of this situation can only be guessed at, and depends on the balance between the invasion rates of *amasina* genotypes and the relative fitness of the hybrids. Theoretically, gene frequencies within the hybrid population should fluctuate, unless at all times exactly as many "*amasina*" genotypes are eliminated from as are imported into the population. If the imbalance between immigration and elimination is large,

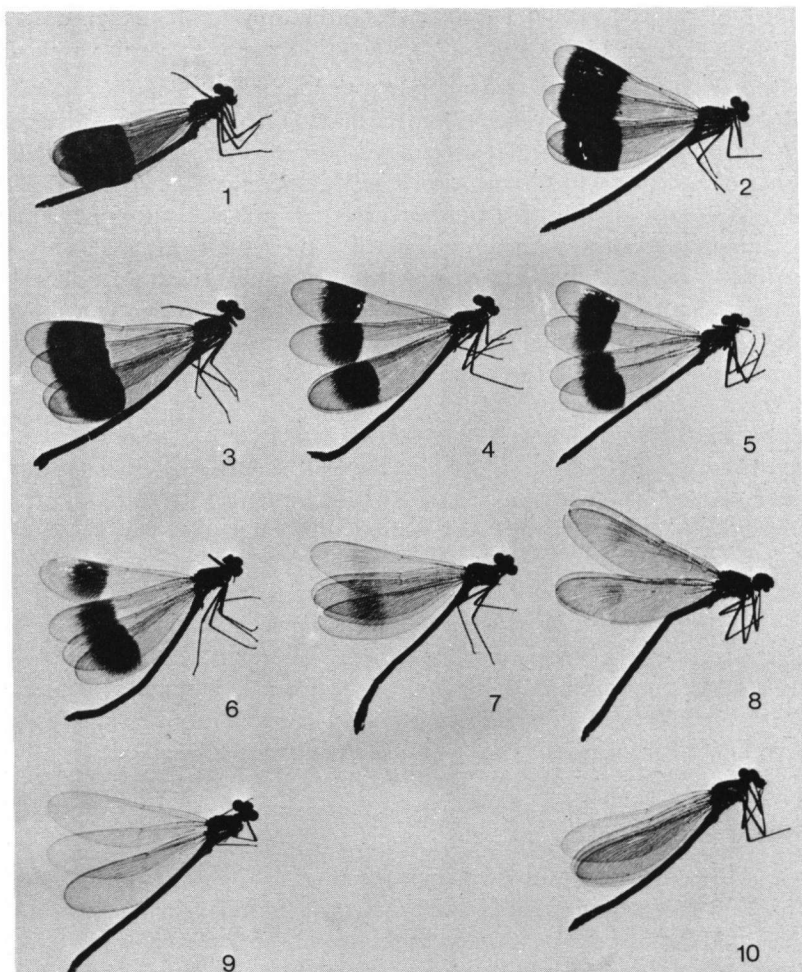


Fig. 2. Comparison of male *Calopteryx* from the hybrid population at Görele, Giresun (2-9): with true *C. s. waterstoni* from Derecik, Trabzon (10) and *C. s. amasina* from Persembe, Ordu (1).

the population will quickly evolve in the direction of either subspecies. If it is small, an apparent stability may result. Only long-term observations may clarify this point. For the time being, we can only state that the Görele population is a *C. s. waterstoni* gene pool, which is supplemented by a limited number of *C. s. amasina* genotypes, or has almost completely displaced a pre-existing *amasina* gene pool from this site.

### THE HABITAT OF *CALOPTERYX SPLENDENS WATERSTONI*

*C. s. waterstoni* breeds in fast-running rivulets draining the northern slopes of the Pontic Alps and flowing directly into the Black Sea in an area where the coastal plain is narrow or interrupted by steep rocky shores between narrow river valleys. The northern slopes of the Pontic Alps, as well as the south-western slopes of the Caucasus Mountains, are subject to heavy westerly rainfall from over the Black Sea, causing overcast weather through much of the summer. Consequently, the rivers hardly get a chance to warm up on their course towards the sea. These low water temperatures, and the absence of wide, slow-running streams are thought to define the environmental requirements of *C. s. waterstoni*, conferring it a competitive advantage over the more thermophilous *splendens*-races that replace it in the west and the north.

*C. s. waterstoni* responds to its cold-water habitat by a delayed emergence and delayed reproductive season. Indeed, at the end of July, numerous last-instar larvae could still be found, showing signs of forthcoming metamorphosis. In the more westerly populations of *C. s. amasina*, only young first-year larvae were collected.

On the southern slopes of the Pontic Alps, a much drier climate prevails, with more sunshine and less cloud cover during summer. Here, like e.g. near Gümüşhane (Fig. 1), a heavy-spotted *C. s. amasina*, and not *C. s. waterstoni* occurs. Thus, it seems convenient to define the divide between the mountain slopes as the southern limit of the range of *C. s. waterstoni*, and the Harşit river (Fig. 1) as the eastern limit of the range of *C. s. amasina* along the Black Sea coast.

### THE STATUS OF THE POPULATION AT TAMARA, USSR

As stated earlier, the Çoruh river limits the range of *C. s. waterstoni* to the east. We have no information about the occurrence of *C. splendens* in its upper course, but its middle course builds a wide, deep canyon with torrential water-flow, in which no *C. splendens* could be found in July 1986. On the coastal plain, we found *C. s. waterstoni* up to the easternmost rivulet on Turkish territory, at Kemalpaşa, about 18 km from the mouth of the Çoruh. The latter is situated in the USSR, and was not accessible to us for study.

BARTENEV (1930) recorded a *C. s. tschaldirica* population at Tamara, a locality seven kilometers north-east of Batum and only 15 kilometers north of the mouth of the Çoruh. However, this subspecies is an altitudinal taxon (see further). Exactly in the same way as hybrids between ssp. "*amasina*" and ssp. *waterstoni* take a *tschaldirica*-phenotype it appears to us that ssp. *waterstoni* might produce intermediate phenotypes as a result of boundary interbreeding with the adjacent *splendens*-subspecies, *C. s. mingrelica* Selys. Although it is difficult to give more than a general interpretation of Bartenef's statement that he

saw "many specimens" of ssp. "*tschaldirica*" at Tamara, it can be assumed that this population showed a more equitable hybrid ratio (less biased towards the *waterstoni*-phenotype) than the one at Görele.

#### THE STATUS OF *CALOPTERYX SPLENDENS TSCHALDIRICA* BARTENEF

The relationship between *C. s. tschaldirica* on one hand, and *C. s. amasina* and *C. s. waterstoni* on the other, remains to be considered. As a result of the discovery of the Görele hybrids in 1985, it had occurred to us that hybrid males, with their reduced wing spots (Fig. 2), look exactly like *C. s. tschaldirica*. Part of our 1986 fieldwork was therefore aimed at determining whether ssp. *tschaldirica*

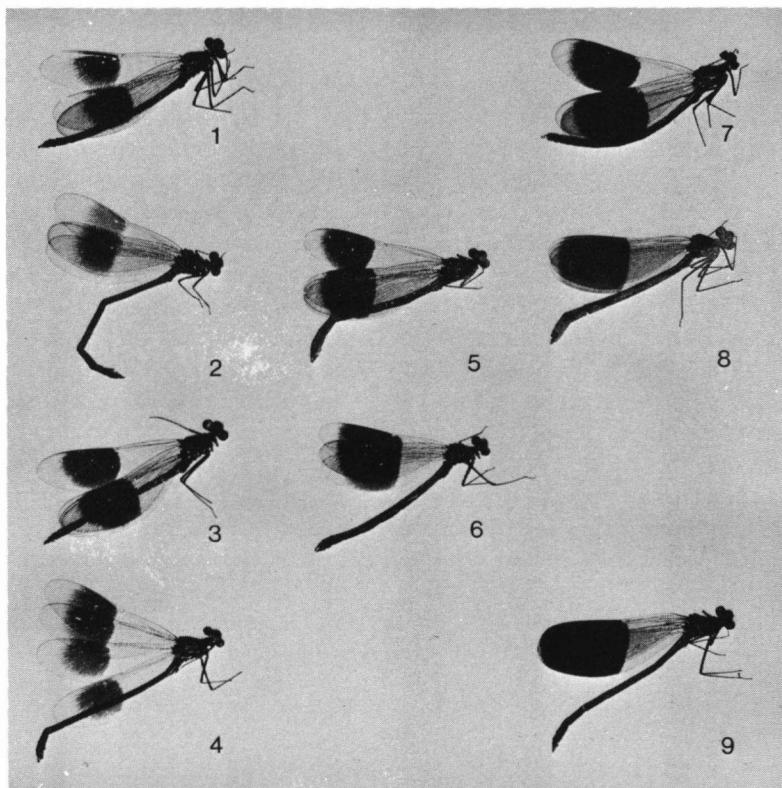


Fig. 3. Comparison of *C. s. tschaldirica* (1-4) with *C. s. amasina* (7-9) and intermediate specimens from the transition zone around Kars (5-6). — (Localities, from NE to SW: Aktaş Gölü [1-2], — Hanak [3], — Ardahan [4], — Arpaçay [5], — Selim [6], — Karakurt [7], — Tercan [8] and Amasya [9], the type locality of *C. s. amasina*).

exists at all, or forms a broad cline between such taxa as *C. s. amasina* and *C. s. mingrelica*. The results (Fig. 3) strongly argue in favour of the reality of ssp. *tschaldirica*. It inhabits the plateau area of south-east Anatolia at altitudes ranging between 1600 and 1800 m. and similar areas in the Soviet Armenian Republic. A cline, providing a smooth transition between *C. s. amasina* and *C. s. tschaldirica* was shown to exist on the upper tributaries of the Kars Çayı around Kars (Fig. 3). This cline is much wider than that between ssp. *amasina* and ssp. *waterstoni*, indicating that the intergradation between various subspecies of the *C. splendens*-group may take a spatial extent which differs from case to case. As stated earlier, the ranges of ssp. *waterstoni* and ssp. *tschaldirica* and the costal record by BARTENEFF (1930) of ssp. *tschaldirica*, must be considered invalid on ecological and distributional grounds.

### CONCLUDING REMARKS

The significance of the present paper goes beyond the mere establishment of the status and range of a few subspecies of the *C. splendens*-complex. It confirms the long-held belief that the size of the male wing spot is a useful genetic marker at the subspecific level, although the amount of intra-subspecies variation in this character remains to be determined for a great number of races. The study presented here stands out by the fact that extreme cases (no wing spot versus a large wing spot) were found in vicariation, and hybrids could be readily identified. In addition, the fact that the cline between ssp. *waterstoni* and ssp. *amasina* was so steep, gave additional confidence in the hybrid nature of the Görele population. However, the cline between ssp. *amasina* and ssp. *tschaldirica*, although less steep, less extreme, and spatially spread over a broader territory, can also be objectively defined.

Our hypothesis is that such results can be generalized over the entire range of the *C. splendens*-complex, which we imagine as a mosaic of spatially delimited subspecies, semispecies, and species, each with a unique geographical range, and bounded by clines of variable steepness. The task that lies ahead is to map out all these ranges as accurately as possible.

Since, as stated in the introduction, the possible amount of variation in wing spot size is limited, a particular wing spot type may have evolved more than once, in disjunct situations, marking different underlying genomes, hence different geographical subspecies. The *tschaldirica*-type, for example, is found in true ssp. *tschaldirica*, but also in ssp. *taurica* from the Crimea, and in a *taurica*-like taxon which has been recorded from Denmark (RIS, 1918); the *waterstoni* phenotype is "repeated" in *C. s. hyalina* Martin from Syria and the Lebanon. Quite a few other examples could be cited.

The wing spot as a practical marker for subspecies is therefore imperfect. It can, apparently, not be supplemented by other morphological markers. Electro-



phoretic measurement of allele frequencies (MAIBACH, 1985) is a useful tool, but restricted to water-soluble enzymes and therefore of limited power. Thus, identification of subspecies of *Calopteryx splendens* (and other, related *Calopteryx*-groups) will henceforth require detailed geographical information. Morphology alone can no longer be acceptable as the sole criterion for identifying taxa in this group of Odonata.

#### ACKNOWLEDGEMENTS

The present study was made possible by NATO-grant no. RG 85/0368 "Zoogeography of Turkey, with emphasis on the Insecta Odonata" to H. Dumont and A. Demirsoy; we also thank Dr NILGUN KAZANCI, Ir NECATI KAZANCI, and Mr LUC BRENDONCK for help in the field. D. Verschuren acknowledges a research grant of the I.W.O.N.K., Belgium.

#### REFERENCES

- BARTENEV, A.N., 1909. [Odonata der Kars-Exkursion]. *Trudy study Kruzh. Izsled. russk. Priro. imp. mosk. Univ.* 4: 63-75. (Russ.).
- BARTENEV, A.N., 1912. [Die palaearktischen und ostasiatischen Arten und Unterarten der Gattung *Calopteryx* Leach]. *Rab. Lab. zool. Kab. imp. warsh. Univ.* 1 1911: 63-257. (Russ.).
- BARTENEV, A.N., 1930. Über *Calopteryx splendens* und ihre Biotypen, besonders die Westasiatischen. *Zool. Jb. Syst.* 58: 521-540.
- BUCHHOLTZ, C., 1955. Eine vergleichende Ethologie der orientalischen *Calopterygiden* (Odonaten) als Beitrag zu ihrer systematischen Deutung. *Z. Tierpsych.* 12: 364-386.
- DEMIRSOY, A., 1979. Türkiye Zoocografyası. *Türkiye Faunası A-Ek*, pp. 1-53. Hacettepe Üniversitesi, Beytepe-Ankara.
- DUMONT, H.J., 1977. A review of the dragonfly fauna of Turkey and adjacent mediterranean islands (Insecta: Odonata). *Bull. Anns Soc. r. belge Ent.* 113: 119-171.
- FOX, D.L., 1953. *Animal biochromes and structural colours*. Cambridge Univ. Press.
- FOX, H.H. & G. VEVERS, 1960. *The nature of animal colours*. Sidgwick & Jackson, London.
- HEYMER, A., 1977. *Ethological dictionary*. Parey, Berlin-Hamburg.
- MAIBACH, A., 1985. Revision systématique du genre *Calopteryx* Leach (Odonata, Zygoptera) pour l'Europe Occidentale. I. Analyses biochimiques. *Mitt. schweiz. ent Ges.* 58: 477-492.
- RIS, F., 1918. Der Artbegriff, insbesondere in der Entomologie. *Mitt. Ent. Zürich* 4: 261-278.
- SCHNEIDER, W., 1984. Description of *Calopteryx waterstoni* spec. nov. from northeastern Turkey (Zygoptera: Calopterygidae). *Odonatologica* 13: 281-286.