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CONTRIBUTION TO THE GENUS SYMPETRUM NEWMAN, 1833 (ODONATA, ANISOPTERA) FROM SW ROMANIA, WITH A GENERAL DISCUSSION ON SYMPETRUM SPECIES

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ABSTRACT

The paper presents the results of an exploratory research on the genus Sympetrum in two regions in the SW part of Romania (Timiş Plain and Oltenia region), in terms of the faunistic account, species distribution and comparative morphology. The variable, constant and distinctive characters are given for each species. The variability of some taxonomic characters – pterostigma, the male accessory genitalia and the vulvar scale is compared with data from the available literature. The analysis reveals that pterostigma variability and set (combinations) of morphological characters (legs and vulvar scale) go out of the current knowledge, questioning their taxonomic value. A discussion on Sympetrum species is provided from the perspective of the classical principles of systematic zoology: the biological species concept, the reproductive isolation of species, species delimitation, speciation.

INTRODUCTION

Sympetrum Newman, 1833 is an Anisopteran genus consisting of around 60 species distributed over most zoogeographical regions except Australasia (Askew 2004). The European fauna counts around 15 Sympetrum taxonomic entities, most of them considered good species, with large and overlapped geographical ranges, extended in some cases on adjacent areas (Asia, N Africa). Of these, some are very well distinct morphologically and unmistakable: *S. danae* (Sulzer, 1776), *S. pedemontanum* (Müller in Allioni, 1766), *S. flaveolum* (Linnaeus, 1758). Some others are very similar morphologically and the distinction between them is based on minor differences as diagnostic characters, or on questionable differences (colour). In such cases the taxonomic status becomes unclear, and one entity comes to be considered a species or subspecies by different authors, for example *S. nigrifemur* (Selys, 1884), *S. nigrescens* (Lucas, 1912), *S. decoloratum* (Selys, 1884) (Askew 2004, Dijkstra et al. 2020, Wildermuth & Martens 2019). The taxonomic statutes and phylogenetic relationships within Sympetrum are subjected to morphological, molecular, and combined studies (for instance Hinojosa et al. 2017, Jödicke 1994, Jödicke et al. 2000, Jödicke et al. 2009, Pilgrim & Dohlen 2007, Pilgrim & Dohlen 2012).

Nine Sympetrum species are cited for the Romanian fauna: *S. vulgatum* (Linnaeus, 1758), *S. striolatum* (Charpentier, 1840), *S. meridionale* (Selys, 1841), *S. fonscolombii* (Selys, 1840), *S. flaveolum*, *S. sanguineum* (Müller, 1764), *S.*

depressiusculum (Selys, 1841), *S. danae* and *S. pedemontanum* (Babalean 2023, Cîrdei & Bulimar 1965, Manci 2012).

The aim of this paper was to broaden the knowledge on the genus Sympetrum with respect to i) species distribution especially for Oltenia region which is much understudied in these terms and ii) the morphological variability of species within and between populations.

MATERIAL AND METHODS

Sympetrum species were collected between June 2022 and October 2023 from the following sites in SW Romania (Fig. 1):

- Timiș Plain: Jimbolia
- Oltenia region (Dolj county): Băilești Plain, Balta Cilieni (near Băilești locality), Maglavit Lake (near Maglavit locality), Siliștea Crucii (on Baboia Stream)
- Romanați Plain: Lișteava Pool, Ostroveni (on Jieț River), Cârna – Bistreț Lakes, several pools and lakes in Craiova locality (Romanescu Park, Balta Craiovițe, Lacul Tanchistului), Preajba Ponds, Bratovoiești (on a small local, low-flowing stream)
- The Getic Piedmont: Filiași Central Lake

The specimens were collected with the entomologic net, introduced into 75° to absolute ethanol, thereafter, removed and stored in 70° ethanol. All the photos were taken by author.

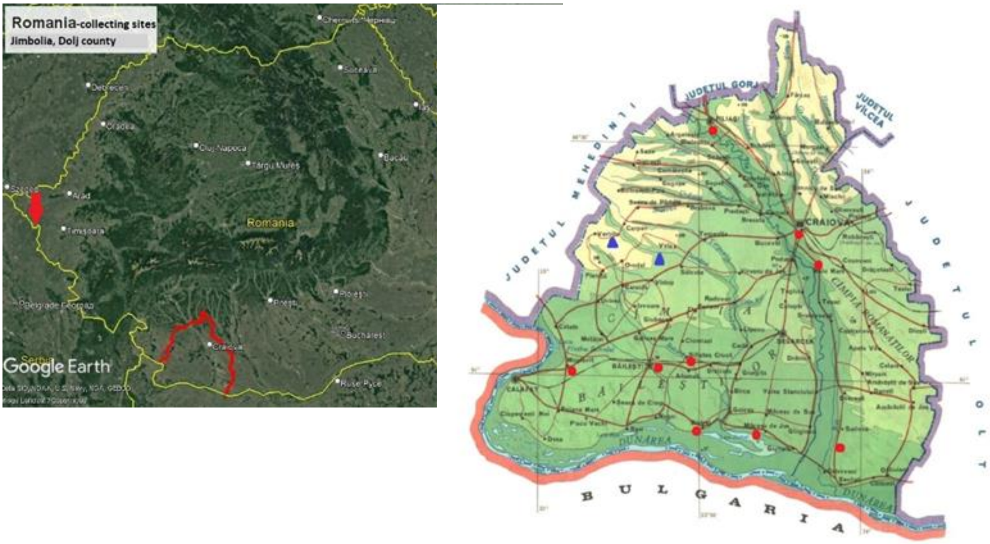

Figure 1. The map of the investigated sites: Jimbolia (red arrow); Dolj county (red dots - collecting sites, blue triangles - sites with detected Sympetrum populations) (maps with Google Earth Pro and Dolj.jpg (1215×1026) (pe-harta.ro))

RESULTS AND DISCUSSIONS

Systematic account and morphology

1) *Sympetrum fonscolombii* (Selys, 1840) – Figs. 2 – 4

Lișteava Pool – 28 July 2022, 1♀

Maglavit Lake – 16 June 2022, 1♂

Brief description: legs: the first pair mostly yellow, the second and third pairs mostly black with a fine yellow dorsal stripe; the amber patch on the male posterior wing barely reaching the base of the discoidal cell; pterostigma yellow with black borders, with asymmetry in male (Fig. 2), on 3 cells in the left forewing and on 2 cells in the right forewing (on 2/3 of a cell and on 1/3 of the other cell), female pterostigma (Fig. 3) on two cells (on 2/3 of a cell and on 1/3 of the other cell); hamular processes (Fig. 4A): a rather short inner anterior process with a black tip, the outer posterior process wide and with a distinctive short triangular extension; vulvar scale (Fig. 4B) with two widely separated lobes, two digitiform prominences on S9 sternite.

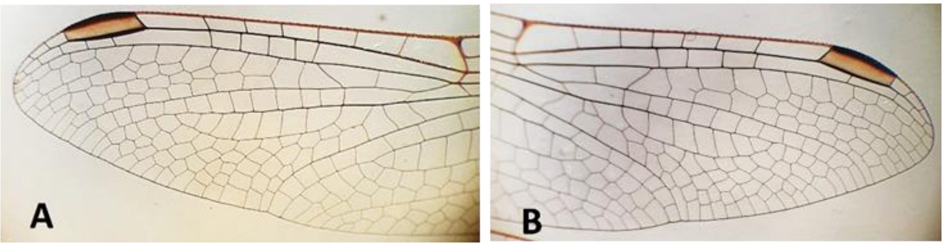

Figure 2. *Sympetrum fonscolombii*, male pterostigma asymmetry on: A - left forewing, B - right forewing

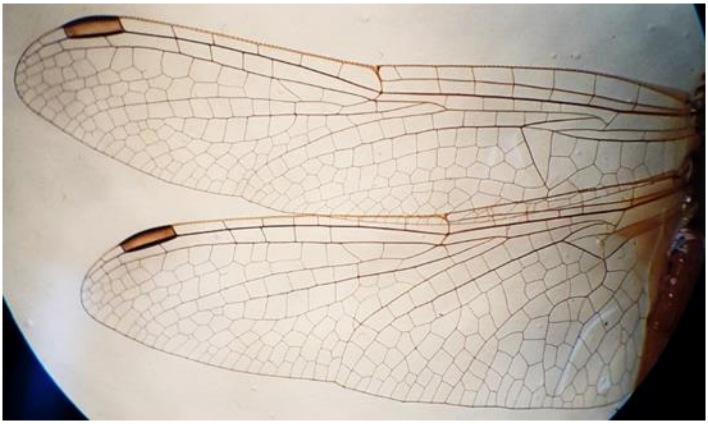

Figure 3. *Sympetrum fonscolombii* - female left wings

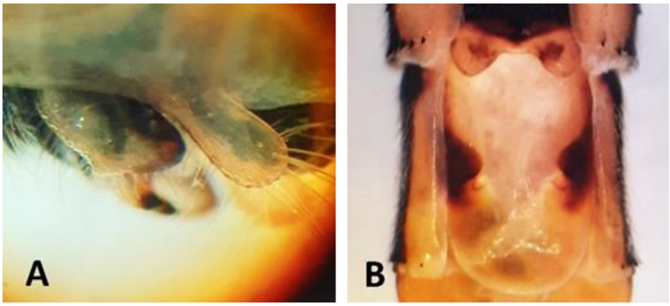

Figure 4. *Sympetrum fonscolombii*, the genitalia, A - the hamules, B - the vulvar scale

2) *Sympetrum striolatum* (Charpentier, 1840) – Figs. 5, 6
Craiova: Romanescu Park – 22 September 2022 (1♂); Balta Craioviței, 25 September 2022, (3♂♂, 1♀); Lacul Tanchistului, 16 October 2022, (8♂♂, 9♀♀)
Filiași Central Lake – 07 October 2022, (2♂♂)
Balta Cilieni, Băilești – 18 October 2022 (1 ♂), 11 September 2023 (1♀ in a heterospecific couple with *S. meridionale* ♂)
Siliștea Crucii – 12 October 2023 (3 couples)
Ostroveni – 16 October 2023 (1♀)

Constant characters: male and female legs predominantly black, with a thin yellow dorsal stripe (Fig. 5A); male and female pterostigma brown; lateral synthorax with two large greenish-yellow bands (Fig. 5A); hamular processes (Fig. 6C) nearly equal: the inner anterior process slender, the outer posterior process wide; vulvar scale (Fig. 6A, B) moderately prominent, with a wide undulation, the sternite below with two digitiform prominences.

Variable characters: the position of the pterostigma is a constant character in all populations, namely, on 2 cells (on one cell entirely and on 1/3 of the second cell), both on forewing and hindwing (Figs. 5B, D), excepting two females from Siliștea Crucii with pterostigma asymmetry, pterostigma over 3 cells both on the right forewing and on the right hindwing) (Fig. 5C).

Distinctive characters: the colour of the legs, the two large greenish bands on side thorax, the vulvar scale.

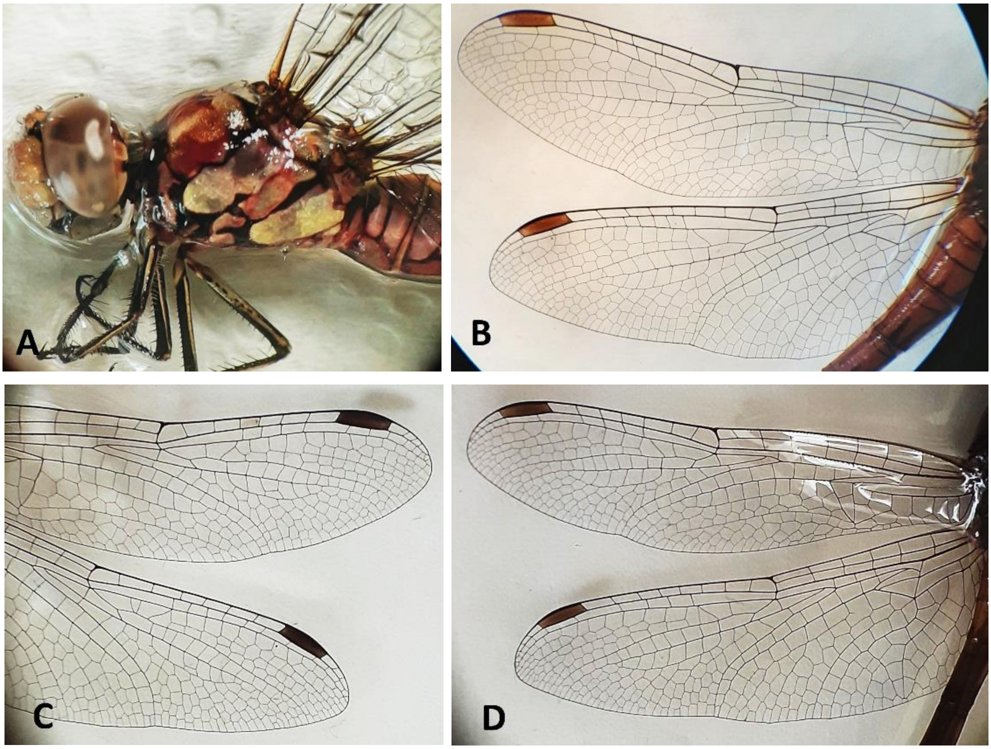

Figure 5. *Sympetrum striolatum*, A - female habitus (Cilieni); B - female left wings (Balta Craioviței); C - female pterostigma asymmetry (Siliștea); D - male left wings (Balta Craioviței)

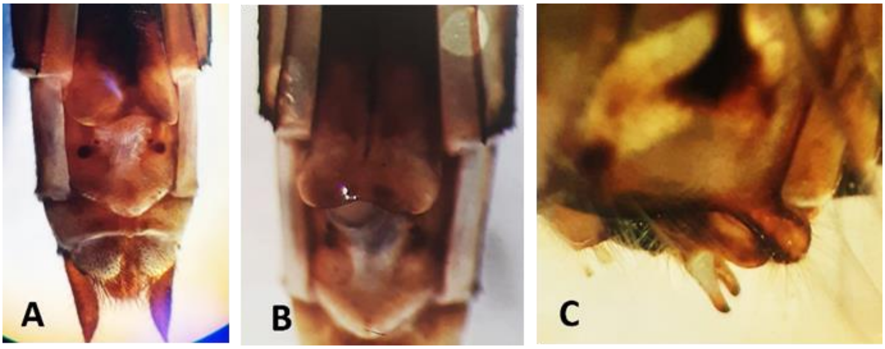

Figure 6. *Sympetrum striolatum*, genitalia, A - vulvar scale (Lacul Tanchistului), B - vulvar scale and egg, specimen from hetero-couple (Cilieni); C - hamules (Balta Craioviței)

3) *Sympetrum meridionale* (Selys, 1841) – Figs. 7 – 9
Balta Cilieni, Băilești – 18 October 2022 (3♂♂, 2♀♀), 11 September 2023 (10 ♂♂, 1♀, 7 couples out of which a heterospecific couple – *S. meridionale* male x *S. striolatum* female)
Preajba – 07 September 2023 (5♂♂)

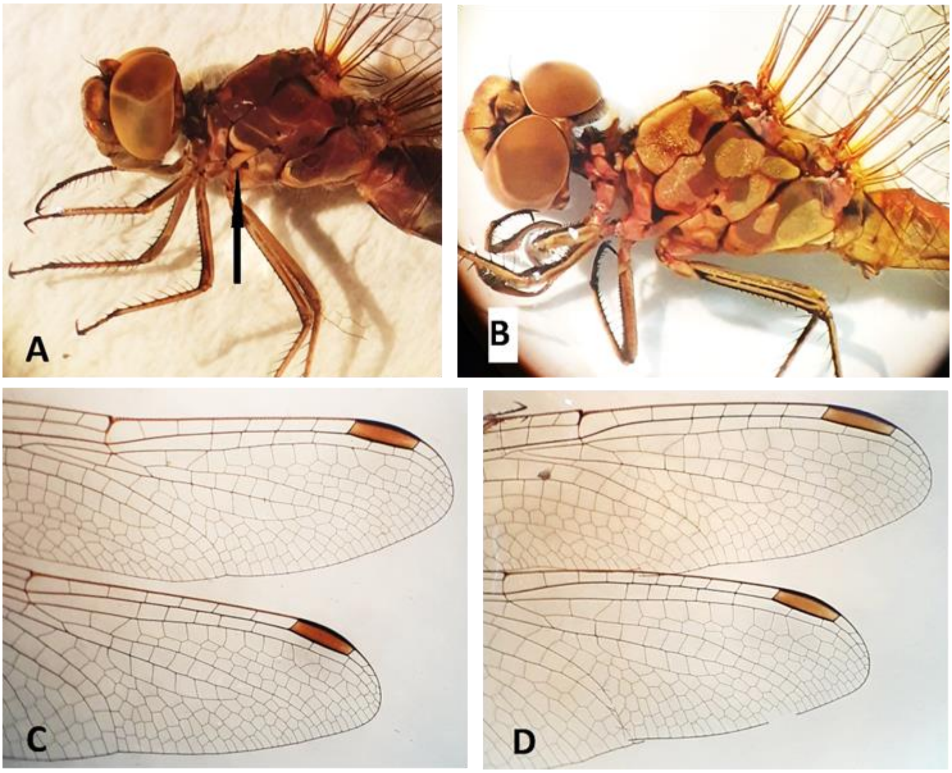

Figure 7. *Sympetrum meridionale*, habitus, A - female habitus (Cilieni), arrow indicating the “delta” spot; B - male habitus (Preajba); C - pterostigma asymmetry, male (Bistreț); D - pterostigma asymmetry, female (Cârna)

Lișteava – 13 September 2023 (one couple)
Cârna – 13 September 2023 (2♂♂, 5♀♀, 3 couples)
Bistreț – 13 September 2023 (2♂♂, 2♀♀)
Bratovoiești – 16 October 2023 (1♀)
Jimbolia – 01-06 August 2022 (agricultural irrigation canal, garden, 3♂, 2♀♀)

Constant characters: male and female legs striped in black and yellow, predominant colour yellow (Fig. 7A, B); pterostigma brown; the black sutures on sides of thorax unmarked or very slightly marked, the mesepimeron with a well visible spot in the shape of the letter "delta" (Δ,► black core, yellow margins) near the junction of mid coxa (Fig. 7A, B) present in all males and females, yellow spiracle with black border, a black point above the spiracle; hamular processes (Fig. 8) rather unequal, the outer posterior process of a long triangle shape, and shorter than the inner anterior process which is slender and ends in a black hooked tip; the general pattern of the vulvar scale – incurved, cup-shaped in lateral view and consisting of two concrescent lamellae, double bifid in ventral view (Fig. 9).

Variable characters: male and female pterostigma position: on 2 – 3 cells, with asymmetry in the same specimen (Fig. 7C, D); the colour pattern on side of thorax in males is an individual combination of brown, red, reddish-purple, and greenish spots of various shapes and sizes.

Distinctive characters: the colour of the legs, the inconspicuous black sutures on lateral thorax, the "delta" spot on lateral thorax in both males and females.

Figure 8. *Sympetrum meridionale*, the hamules, male (Cilieni)

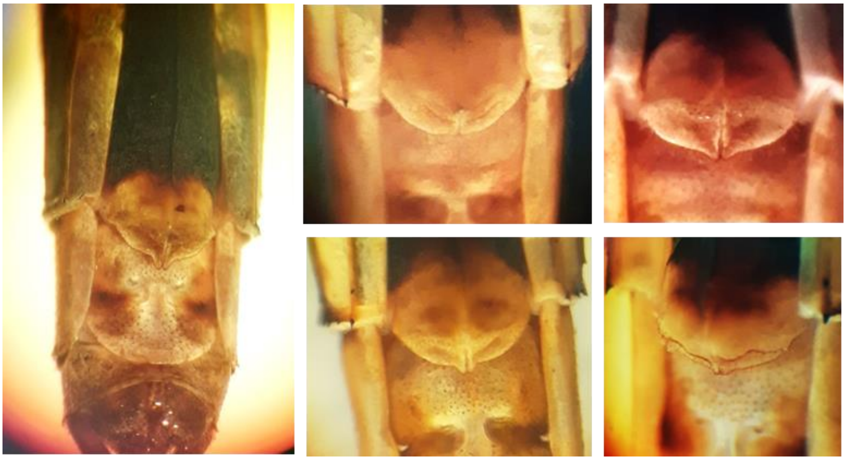

Figure 9. *Sympetrum meridionale*, the general bifid pattern of the vulvar scale in females from various populations (Cilieni, Cârna, Jimbolia)

4) *Sympetrum sanguineum* (Müller, 1764) – Figs. 10 – 13
Craiova – Romanescu Park, 18 August 2022 (5♂♂), 07 September 2022 (2♂♂, 1♀), 22 September 2022 (2♂♂, 1♀)
Jimbolia, 06 August 2022 (2 ♀♀, 1 ♂ from a completely dry irrigation canal, habitat shared with *S. meridionale*); 07 August 2022 (4♂♂ from the vegetation of a small pool near the Jimbolia recreational swimming pool).

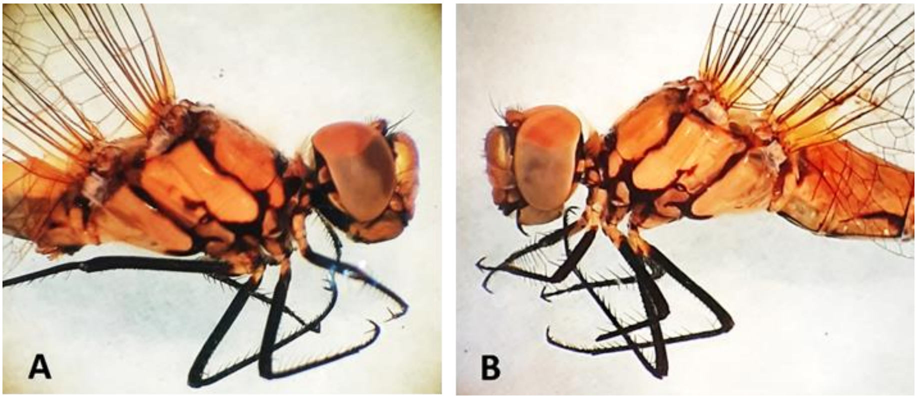

Figure 10. *Sympetrum sanguineum*, habitus, A - male (Jimbolia), B - female (Jimbolia)

Constant characters: black legs (Fig. 10); thorax with conspicuous black lateral sutures; the pattern of the hamular processes, of about equal length, the inner process has a curved black tip, the outer posterior process long ovoid (Fig. 12); the ovipositor very well visible in lateral view, incurved, with a deep concavity (Fig. 13A, B), bifid, consisting of two concrescent lamellae visible in ventral view (Fig. 13C, D).

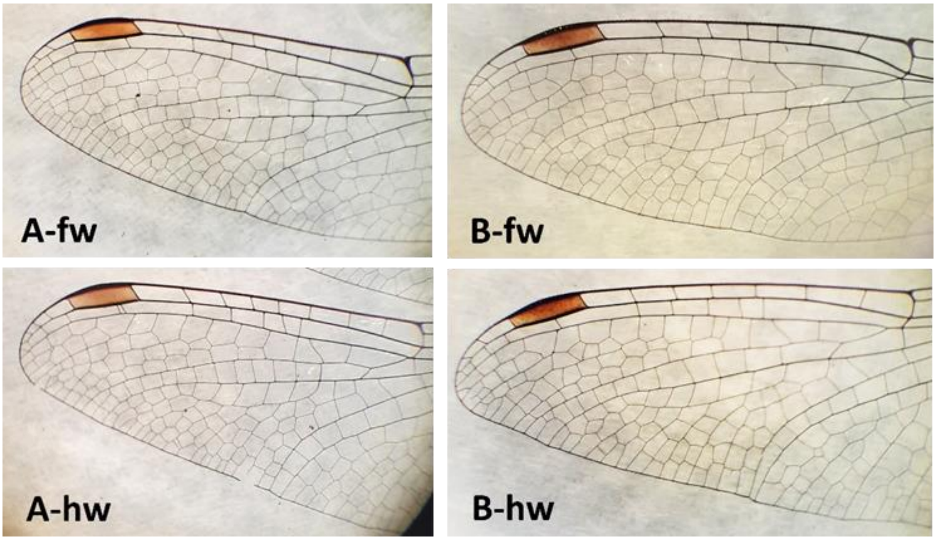

Figure 11. *Sympetrum sanguineum* pterostigma, A - male pterostigma on forewing (fw) and hindwing (hw) (Jimbolia); B - female pterostigma on forewing and hindwing (Jimbolia)

Variable characters: the position of the pterostigma: male pterostigma (Fig. 11A) on two cells, female pterostigma (Fig. 11B) on 2 cells – on 1/3 of a cell and on 2/3 of the other cell; the position of pterostigma is very little variable, with low asymmetry in some specimens.
Distinctive characters: the black legs, the black sutures on side thorax.

Figure 12. *Sympetrum sanguineum*, the hamules (specimen from Jimbolia)

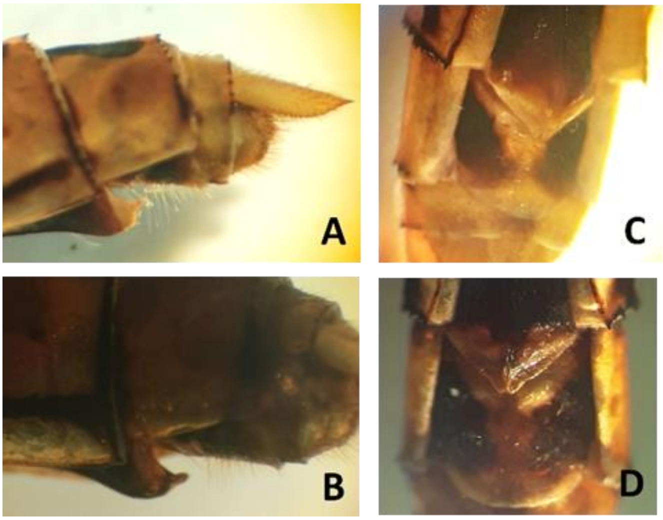

Figure 13. *Sympetrum sanguineum*, the ovipositor in lateral and ventral view: A, C - specimen from Jimbolia; B, D - specimen from Craiova

5) *Sympetrum vulgatum* (Linnaeus, 1758) – Fig. 14
Ostroveni, 16 October 2023 (one couple)

Short description: legs in male and female (Fig. 14A) predominantly yellow on dorsal and mostly black on ventral, with a yellow band, smaller in male; side of thorax very similar to that of *S. meridionale* (of this paper), with greenish and red spots; a “delta” spot similar to that of *S. meridionale*, but not very distinct, present in male and female (Fig. 14A); pterostigma on 2 cells (Fig. 14B); the hamules (Fig. 14C), with the external hamule rather distinct in lateral view, broad and rectangular, not identical to that of *S. vulgatum* as figured by Askew (2004, pg. 174, fig. 316); the vulvar scale (Fig. 14D, E) typical for *S. vulgatum* as figured in literature, almost perpendicular on the sternite.

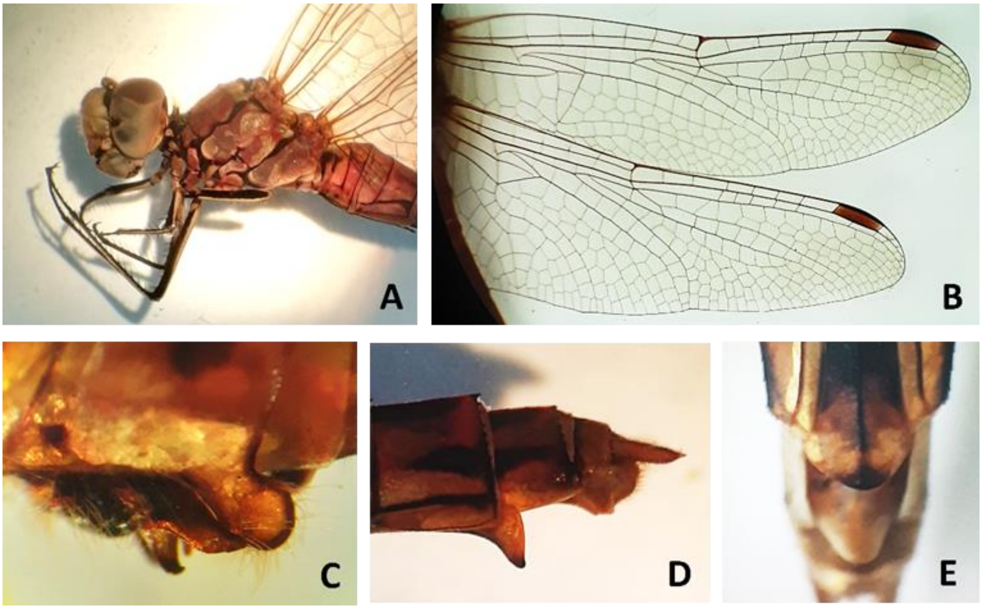

Figure 14. *Sympetrum vulgatum*: A - female habitus (Ostroveni); B - male wings (Ostroveni); C - hamules; D, E - vulvar scale in lateral and ventral view

Sympetrum species assemblages
- *S.meridionale* and *S. sanguineum* – Jimbolia
- *S. meridionale* and *S. striolatum* – Romanescu Park, Cilieni
- heterospecific couple – *S. meridionale* male x *S. striolatum* female – Cilieni
- *S. striolatum* and *S. vulgatum* – Ostroveni

Discussions

Comparative morphology

S. striolatum corresponds to the morphological descriptions of the literature (Askew 2004, Boudot et al. 2019, Cîrdei & Bulimar 1965, Dijkstra et al. 2020, Smallshire & Swash 2020, Wildermuth & Martens 2019). Excepting the females from Siliștea Crucii, with pterostigma asymmetry over 3 cells, *S. striolatum* shows the highest constancy of all characters within and among populations.

Regarding the species *S. fonscolombii*, the collected male specimen reveals asymmetry of the pterostigma on the left and right forewings. The arrangement of the pterostigma on 3 cells in the left forewing (Fig. 2) is similar with *S. depressiusculum* (Askew 2004, pg.175, fig. 347) but such an arrangement in a single individual should be considered rather incidental. The position of the pterostigma on 2/3 of a cell and on 1/3 of the second cell on the right wing is characteristic (species specific) for *S. fonscolombii* male in Boudot et al. (2019) pterography. The broad and distinct outer hamular process (with the triangular extension) slightly deviates (removes) the collected specimen from the species *S. fonscolombii*, as drawn by Askew (2004, pg. 174, fig. 321). The internal hamular process is more similar with that of *S. flaveolum* (Askew 2004, pg. 174, fig. 322) in its length and the slightly hooked apex (Fig. 4A). The colour of the legs is a distinctive character and fits the illustrated description elsewhere (Jödicke & Borkenstein 2022).

For the collected specimens (*S. sanguineum*) of this paper:

- the accessory genitalia correspond to the description of the literature for *S. sanguineum* (Askew 2004, Dijkstra et al. 2020, Hoess 2003)
- the bifid vulvar scale differs from that presented in most literature, both in lateral and especially in ventral view: not too prominent in lateral view (Hoess 2003); “neither prominent, nor bilobed” (Askew 2004); with a visible, rounded, not-bifid tip (Cîrdei & Bulimar 1965). Only Dijkstra et al. (2020) present a bifid vulvar scale with a very short, rounded apex, very shortly bifid.

S. meridionale is the most variable species in terms of several characters:

- an important variability of the pterostigma, with asymmetry (placed on 2 – 3 cells) in the same individual and in different populations. The position of the pterostigma on 3 cells is again similar with that of *S. depressiusculum* (Askew 2004, pg.175, fig. 347).
- the accessory genitalia correspond with the variability presented in the literature (Askew 2004, Cîrdei & Bulimar 1965, Dijkstra et al. 2020, Hoess 2003)
- the vulvar scale is well visible in lateral view in at least half of the specimens and thus it may be considered moderately prominent. In ventral view, the vulvar scale shows the same bifid pattern in all collected specimens (two overlapping concrescent lamellae, both bifid). This aspect differs from that presented in the odonatological literature: not prominent in lateral view (Hoess 2003); “scarcely visible in lateral view” and illustrated straight, not bifid (Askew 2004); “very small” and illustrated with a small median plate flanked by two plates (Cîrdei & Bulimar 1965, fig. 222, pg. 246); “appressed in *S. meridionale* typical” (Dijkstra et al. 2020).

Three morphological aspects are to be remarked:

Once, it is the presence of the same bifid pattern of vulvar scale in both specimens with black legs (typical for *S. sanguineum*) and specimens with striped legs (typical for *S. meridionale*), see Figs. 9 and 13,

The second is the pterostigma asymmetry: in some individuals, its occurrence in different populations, and pterostigma position on 3 cells in four different species – *S. fonscolombii*, *S. meridionale*, *S. striolatum* (of this paper) and *S. depressiusculum* (literature),

The third aspect is the same position of female pterostigma on 2 cells (on 2/3 of one cell and on 1/3 of the second cell) in three different species: *S. fonscolombii*, *S. meridionale* forewing and *S. sanguineum* (of this paper – Figs. 3, 7D, 11B).

These three aspects indicate a problem of the genus Sympetrum in species diagnosability or even in species composition, suggesting either hybridization or other unknown mechanisms by which such a variability and character combinations occur.

Speciation biology

The discussion from now on will consider the classical principles of systematic zoology: the species concepts, speciation process and mechanisms, the reproductive isolation of species in Odonata, and issues in species delimitation.

Species concepts

During time, several species concepts evolved, for instance the biological species concept (BSC), ecological, evolutionary, phylogenetic species concepts (PSC), etc. (De Queiroz 2007). Of them all, the species viewed through the BSC is the only objective taxonomical unit that corresponds to a natural community. It is the reproductive isolation per se that gives the objectivity. Species seen through other concepts implies different degrees of subjectivity.

According to Mayr definition, a species is “a group of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups” (Bănărecu 1973). This definition represents the biological species concept (BSC). The BSC and PSC are closely, indissolubly correlated, a good species has an origin and phylogenetic relations with other species.

Speciation biology

Deciphering the mechanisms of the speciation process is one of the most interesting biological issues, giving rise to a new discipline – the speciation biology. Speciation is seen as a continuous process but most important, it is also seen as a reversible process, where “reproductive isolation can be accumulated or lost; relatively divergent species pairs may collapse owing to hybridization” (Coughlan & Matute 2020).

The reproductive isolation of species in Odonata is still a matter of debate.

Several types of isolating barriers are incriminated in species reproductive isolation in Odonata:

1) premating isolating barriers: temporal isolation (differences in flight season and diel reproductive periods); habitat isolation or microgeographic isolation; ethological or behavioural isolation (by visual stimuli, tactile stimuli, olfactory and auditory stimuli); mechanical isolation with 3 suggested types – incompatibility of genitalia (the lock-and-key hypothesis), incompatibility in tandem linkage involving the anal appendages, and sperm removal involving the shape and length of the penis (Barnard et al. 2017 and Isaacson 2017, Frati et al. 2015, Tennessen 1982 and included references).

2) postmating isolating barriers – the spermatozoa, fertilization, …. (Sánchez-Guillén et al. 2011).

3) a more recent category of isolating barriers are the intrinsic postzygotic barriers which can contribute to speciation in multiple ways (Coughlan & Matute 2020).

In different groups of Odonata, the first two isolating barriers may “operate in sequence, or series, one reinforcing another”, nevertheless the premating barriers are considered not being 100% effective (Tennessen 1982 and included references), but they are “key factors in preventing gene flow between species” (Sánchez-Guillén et al. 2011).

Mate recognition (species specific mate recognition) is not always efficient, thus, heterospecific, intergeneric and even inter-family pairings are not uncommon, being reported both in damselflies and dragonflies under natural conditions (for instance Bick & Bick 1981, Dey & Pal 2022, Frömel & Frank 2020, Rehfeldt 1993, Thio & Ngiam 2023, Wildermuth 2015) and in laboratory (for instance Okude et al. 2020). Heterospecific mating with subsequent oviposition was reported by Kunz (2010) in Orthetrum and Sympetrum.

Neither hybridization is uncommon within Odonata. Hybridization between Ischnura species was reported, and an incipient reproductive isolation was suggested (Monetti et al. 2002 and included references, Schneider & Krupp 1996). Tennessen (1982) gives a list of 15 dragonfly species reported to have produced hybrid individuals. Molecular evidence for hybrid zones is synthesized by Sánchez-Guillén et al. (2023) and Wellenreuther et al. (2023).

The species of the genus Sympetrum are involved both in heterospecific pairing (Bick & Bick 1981, Kunz 2010, Rehfeldt 1993, Wildermuth 2015) and hybridization (Tennessen 1982).

Issues in species delimitation (and phylogenetic analysis)

Species delimitation is a matter of great importance in systematic biology and not only. Much has been written on the value, subjectivity, and limits of phenotypic data and of molecular markers in species delimitations. The purpose of this work is not the history of methods in species delimitation, and debates on these topics can be found in the following few examples of representative literature on various taxa: Cadena et al. 2018, De Salle et al. 2005, Markolf et al. 2011, Ožana et al. 2022, Rokas & Carroll 2005, Sukumaran & Knowles 2017, Wiens 2004. In the case of Odonata it is known that “unavailability of detailed knowledge forces taxonomists to apply more practical criteria to define species” (Dijkstra & Kalkman 2012).

Species delimitation on morphological characters

The firsts, main and most important morphological characters used in species delimitation in most arthropod taxa are the genitalia because they are the characters involved in reproduction and thus, closest to the analysis of reproductive isolation. Nevertheless, this association (genitalia – reproductive isolation) should be done with much care for each analysed taxon because at least in theory even the genitalia can be affected by the cryptic (cryptic species at the genitalia levels – identical genitalia but good species, reproductively isolated at a different level). Other characters, for example the shape and the colour of various parts of the body are used as secondary characters (as set of characters) in species description and species identification.

The sex-involved structures in Odonata are the anal appendages, the male accessory genitalia (hamules) and the vulvar scale. The male anal appendages were hypothesized to be found important in mechanical isolation in species where they *differ substantially* (Paulson, 1974). The male anal appendages in Sympetrum species are so similar that they can be considered to have no role in species reproductive isolation. The delimitation of some Sympetrum species is based on critical small differences of the genitals – hamules and vulvar scale, as diagnostic characters (Askew 2004). For two reasons, species delimitation on such characters is highly subjective: i) the small critical differences and ii) the lack of evidence for the key and lock hypothesis. The use of morphology alone in species delimitation can be misleading – on the one hand, morphologically cryptic species can be seen as only one species, on the other hand, entities with different morphology can in fact be only one species, for instance *S. frequens* and *S. depressiusculum* (Sawabe et al. 2004).

The interpretation of the *S. meridionale* and *S. sanguineum* populations (subject of this paper) can only be subjective and assumptive at the current state of knowledge:

In the specific case of *S. meridionale* of this paper, the local populations with bifid vulvar scale may be seen as a distinct morphological entity, either with a taxonomic rank (good species in a *meridionale* complex) or just a distinct type of population, with different morphological characters. Until supplementary studies, the bifid double-plate pattern of vulvar scale should be considered characteristic for *S. meridionale* populations occupying the presented region. Populations elsewhere in Europe may have a different aspect of the vulvar scale. A similar analysis for the *S. sanguineum* of this paper.

Such local populations are intraspecies subunits that can speciate (it is well known that speciation occurs at the populational level) and they should be comparatively investigated (morphologically, molecularly, ecologically, biologically) with other local populations elsewhere. In case of differences between them, such populations could be considered *differentiated populations*, term introduced by Hahn (Sánchez-Guillén et al. 2023).

However, the problem of the identity of the bifid pattern of the vulvar scale in specimens with black legs (*S. sanguineum*) and striped legs (*S. meridionale*) can only be speculated at this point.

Issues in *Sympetrum* species knowledge

● The speciation mechanisms are not known in Sympetrum.

Bănărescu (1973) makes a clear distinction between *speciation* and *evolution* of a species. *Speciation* is defined as species formation (or the formation of a species). *Speciation* can occur in two ways: i) "splitting of one species in two daughter species e.g. the appearance of a reproductive isolation within a former reproductive community" or ii) by formation of a new species from a pre-existent one, the pre-existent one continuing to exist. Thus, the speciation process "correspond with the formation of a sexual barrier within a former reproductive community" and implies reproductive isolation. Instead, *evolution* of a species is an event at the geological time scale, representing a "deep transformation of species genetic structure and phenotype in time", where the reproductive isolation is not involved. The genetic fond of one species is in permanent fluctuation, "new mutations appear and new populations with a different genetic structure emerge; other mutations disappear, other populations disappear" (Bănărescu 1973).

In the light of the above, the emergence of morphologically differentiated populations (for instance the Sympetrum populations with females with atypical bifid vulvar scale) may be part either of the *speciation* process or of a *species evolution in time*. Species evolution in time could be valid for many Odonata, it may occur at a high speed, meaning a rapid change of the genetic structure expressed in a rapid change of the morphological characters. The natural outcome is the description and naming of numerous new species, the origin of the great diversity the researchers are seeing, over 6000 species (Paulson 2019).

Bănărescu (1973) considers doubtful the possibility of sympatric speciation in biparental organisms but he makes no reference to Odonata. Instead, Battin (1993) brings in discussion literature that "demonstrated in quantitative genetic that a behaviour – the female choice alone can lead to speciation even in the presence of moderate gene flow", that is sympatric speciation. Battin (1993) describes a subtle mechanism that prevent excessive gene flow.

● Some aspects of interspecific hybridization:

Bănărescu (1973), citing Mayr 1963, presents 3 types of interspecific hybridization with importance for the speciation process:

- introgression – hybridization between sympatric species, giving viable and fertile offspring out of which some of them cross with one or both parental species. This type of hybridization is viewed possible between *S. vulgatum* and *S. decoloratum* (Hinojosa et al. 2017). The result is the incorporation of genes belonging to one species into the gene pool of another species.
- mass hybridization between sympatric species with the emergence of a hybrid swarm or a hybrid population.

Most of the European Sympetrum species are sympatric, with a large areal. In the case of two morphologically very similar species (for instance *S. sanguineum* and *S.*

depressiusculum), any of the two above interspecific hybridization types would be difficult to be morphologically measured.

- species formation (speciation) through hybridization followed by alloploidy.

These aspects are not enough documented for Sympetrum.

Sánchez-Guillén et al. (2013-2014) give a new perspective of genetic methods in predicting reproductive isolation in Odonata. Córdoba-Aguilar et al. (2023) give the most comprehensive and modern insights into the power of genomics and genetic markers approaches for seeing and understanding the odonates as a whole – morphology, biology, ecology, biogeography, speciation, phylogeny.

CONCLUSIONS

The morphology of Sympetrum species is characterized by variability and a low constancy of some taxonomic characters which are shared by more species. The background, origin and nature of this variability is unknown and important questions are to be answered: where the morphological variability comes from? Is it genetically stable, for how long in time?

The speciation mechanisms are unknown for the species of the genus Sympetrum.

The heterospecific pairing, the occasional hybridization and the great morphological variability suggest an inefficient and incomplete species reproductive isolation.

Until sufficient data will be accumulated, we can only hypothesize: because of sympatry and lack of perfect reproductive isolation, speciation it is not or cannot be 100% completed. At a large scale in space and time, the genus Sympetrum might be represented by a mixture of differentiated populations, incipient species, subspecies, and good species, with a stronger or lower gene-flow allowing periodic and random species collapse.

Tennessen's (1982) question "how do organisms speciate" and Battin's (1993) question "what a species actually is in odonates" are still actual for the genus Sympetrum.

In the context of a great morphological variability, the presentation of local populations characters is important for further comparative studies.

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