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August 31, 2023
Contribution to the genus Sympetrum Newman, 1833 (Odonata, Anisoptera) from SW Romania, and an analysis of the European species

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Abstract
The paper presents the results of a faunistic investigation on the genus Sympetrum in two regions in the SW part of Romania – Timiș Plain (Banat region) and Oltenia region. The faunistic account comprises four species: Sympetrum fonscolombii (Selys, 1840), Sympetrum striolatum (Charpentier, 1840), Sympetrum sanguineum (Müller, 1764) and Sympetrum meridionale (Selys, 1841). The genitalia of the collected species are compared with data from the available literature. Following, an analysis of the European Sympetrum species is provided from the perspective of the classical principles of systematic zoology: the biological species concept, the reproductive isolation of species in Odonata, species delimitation, speciation.

Introduction
Sympetrum Newman, 1833 is a genus consisting of around 60 species distributed over most zoogeographical regions except Australasia (Askew 2004). Europe counts about 12 species, most of them with large and overlapping geographical ranges. Some of the species are very well distinct morphologically and unmistakable: S. danae (Sulzer, 1776), S. pedemontanum (Müller in Allioni, 1766), S. flaveolum (Linnaeus, 1758). The distinction between others is based on minor differences or on questionable differences – colour. Based on morphology only, many Sympetrum species and subspecies were described and named in the last two centuries in Europe. Their taxonomic status and the phylogenetic relationships are now a continuing debate using morphological, molecular, and combined data/methods (for instance Jödicke 1994, Jödicke et al. 2000, Jödicke et al. 2009, Sawabe et al. 2004, Pilgrim & Dohlen 2007, Pilgrim & Dohlen 2012, Hinojosa et al. 2017).


The faunistic investigation was carried in two regions: Timiș Plain (in Timiș district) and Oltenia region (Dolj district), SW Romania. Especially the Sympetrum fauna of Oltenia region is understudied in terms of species account and distribution.

Material and method
Sympetrum species were collected from sites in:

Timiș Plain:
- Jimbolia

Oltenia region:
Băilești Plain
- Balta Cilieni (Cilieni Lake/Pool), near Băilești locality
- Maglavit Lake, near Maglavit locality
- Romanâti Plain
  - Lișteava Pool, near Căciulătești locality
  - several pools and lakes in Craiova locality: Romanescu Park, Balta Craioviței (Craiovița Pool), Lacul Tanchistului (Tankman Lake/Pool)
- Getic Piedmont
  - Filiași Central Lake

The specimens were collected between June and October 2022 with the entomologic net, in 75° to absolute ethanol, thereafter, removed and stored in 70° ethanol. Additional collections are planned for September 2023.

**Results**

Unpublished results are posted on bioRxiv: [https://doi.org/10.1101/2022.09.17.508356](https://doi.org/10.1101/2022.09.17.508356) and [https://doi.org/10.1101/2022.10.31.514645](https://doi.org/10.1101/2022.10.31.514645)

**Discussions**


For *S. sanguineum* of this paper:
- the accessory genitalia correspond to the description of the literature for *S. sanguineum* (Hoess 2003, Askew 2004, Dijkstra et al. 2020)
- the vulvar scale is presented differently in the literature: not too prominent in lateral view (Hoess 2003); “neither prominent, nor bilobed” (Askew 2004); shortly prominent and bilobed / bifid (Dijkstra et al. 2020); shortly prominent, not bilobed (Cîrdei & Bulimar 1965). The meaning and taxonomic value of the bifid vulvar scale in the females collected from distant populations (Jimbolia, Craiova) is difficult to establish. At the current state of knowledge only hypotheses can be made:
  1) a stable character in different populations: new species or subspecies / only one species with dimorphic females or two sibling species with identical males?
  2) the bifid vulvar scale is characteristic of old females: no taxonomic value
  3) part of the intraspecific variability
  4) other meaning?

For *S. meridionale* of this paper:
- the accessory genitalia correspond with the variability presented in the literature (Cârdei & Bulimar 1965, Hoess 2003, Askew 2004, Dijkstra et al. 2020)
- the vulvar scale is prominent (well visible) in lateral view and bifid in ventral view in both collected specimens from Cilieni Pool. 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 / bilobed (Askew 2004); “very small” and illustrated with a small median plate flanked by two plates (Cîrdei & Bulimar 1965, fig. 222, pg. 246) and “appressed in *S. meridionale* typical” (Dijkstra et al. 2020).

Even more, in one of the two females from Cilieni Pool (*S. meridionale*), the bifid vulvar scale is similar almost to identity with the vulvar scale of *S. sanguineum* collected from Jimbolia-Craiova. The presence of an identical/very similar bifid vulvar scale in two females,
one with black legs (typical for *S. sanguineum*) and the other with predominantly yellow legs (typical for *S. meridionale*) indicates an issue upon which only hypotheses can be made:
1) the result of heterospecific breeding
2) a new taxon
3) the bifid vulvar scale is characteristic of old females — no taxonomic value
4) other meaning?

The discussions from now on will consider 3 aspects: the species concepts, 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. The other taxonomical units are subjective – they are subjected to human mind, definitions, methods, interpretations, etc.

According to Mayr definition, a species is “a group of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups” (Bânărecescu 1973). This definition represents the biological concept species – BSC.

The BSC and PSC are closely, indissolubly correlated – a good species has an origin and phylogenetic relations with other species.

**The reproductive isolation of species in Odonata**

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 (Tennesen 1982 and included references, Frati et al. 2015, Barnard et al. 2017 and Isaacscon 2017).

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

In different groups of Odonata, these isolating barriers may “operate in sequence, or series, one reinforcing another”, nevertheless the premating barriers are considered not being 100% effective (Tennesen 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 and were reported both in damselflies and dragonflies (Bick & Bick 1981, Rehfeldt 1993, Wildermuth 2015, Dey & Pal 2022, Thio & Ngiam 2023). 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). Tennesen (1982) gives a list of 15 dragonfly species reported to have produced hybrid individuals. Molecular evidence for hybrid zone is most probably given in many papers.
The species of the genus Sympetrum are involved both in heterospecific pairing (Bick & Bick 1981, Rehfeldt 1993, Kunz 2010, Wildermuth 2015) and hybridization (Tennessee 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 evolution and history of methods in species delimitation and debates on these topics can be found in the following few examples of representative literature: Wiens 2004, De Salle et al. 2005, Rokas & Carroll 2005, Markolf et al. 2011, Cadena et al. 2017, Sukumaran & Knowles 2017, Ožana et al. 2022.

Species delimitation on morphological characters

In most metazoan taxa, the first, main and most important morphological characters used in species delimitation are the genitalia because they provide 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 should be used as secondary characters in species description and species identification (unless /with the exception these characters intervene in mate recognition – for instance wing transparency in Calopteryx). At the most, such characters should be used for subspecies delimitation, where the genital characters are identical.

In Odonata, the reproductive isolation of species is still a matter of debate. The sex-involved structures: the anal appendages, the male accessory genitalia (hamules) and maybe the vulvar scale are those structures operating at the tactile and mechanical level of the reproductive isolation. In Sympetrum, a potential role of the prothoracic lobe is unknown – what is the role of the prothoracic lobe, why does it exist?

With respect to the anal appendages, male accessory genitalia and vulvar scale, the minor differences (high similarity) between *species* can be considered differently: i) as intraspecific variability of only one species, ii) cryptic species, iii) they have a minor role or have no role in reproductive isolation. In Sympetrum, the male abdominal appendages (anal cerci) are neglected (understudied) and with few exceptions, they are not illustrated.

Odonata literature recognize the accessory genitalia as the diagnostic characters at species level (Askew 2004). Askew’s recognition has a general value, it is not affirmed for Sympetrum species. The key-and-lock hypothesis was neither demonstrated nor inirmed (disproved) for Sympetrum species. Thus, the use of the hamules as species diagnostic is rather problematic. The current taxonomical practice uses the hamules (and the vulvar scale) in species identification.

**Analysis of the European Sympetrum taxonomic entities based on literature, and the subjectivity in establishing the taxonomic level/rank (species/subspecies) using genitalia morphology and the geographical range.**

The literature presents several European Sympetrum taxonomic entities which are differently considered by different authors (species/subspecies) – Table 1
The species analysis starts from the premises:
- when more taxonomic entities (“species”) have the geo-ranges largely overlapped and genitalia (in case it is the main morphological character that prevents hybridization) do not differ between “species”, then the taxonomic entities are to be considered only one species,
- two taxonomic entities with small not-overlapped geographical ranges, and with identical genitals are two populations (or two subspecies) of only one species,
- when for 3 – 4 taxonomic related (with similar but not identical genitalia) entities (“species”), the geographical distribution pattern consists of one large area and 2 – 3 peripheral areae very little overlapped or not overlapped, then the taxonomic entities are to be considered good, distinct species. Such geographical range pattern is characteristic for some newly formed species (Bănărescu 1973).

The geographical range splits the Sympetrum taxonomic entities in 2 major groups:
**G. I. group** – includes 9 species with a very large geographical range and a certain degree of sympatry: *S. fonscolombii, S. flaveolum, S. pedemontanum, S. depressiusculum, S. vulgatum, S. meridionale, S. sanguineum, S. striolatum, S. danae*.

**G. II. group** – includes taxonomic entities (species / subspecies) with limited geo-range: *nigrifemur, nigrescens, decoloratum, sinaiticum, tibiale, ibericum, haritonovi*.

The accessory genitalia and the vulvar scale within **G. I. group**

In the current taxonomical practice, the male accessory genitalia are considered distinct for each species, with various aspects of the external and internal processes: long and slender, short, curved, straight, robust, hooked, stout – stouter. The degree of similarity of the hamules between species is high – “the critical features are small” Askew (2004). The differences between authors’ descriptions are minor but still there are. They might be attributed to the

<table>
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<tr>
<th>Species</th>
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<th>Askew 2004</th>
<th>Wildermuth &amp; Martens 2019</th>
<th>Dijkstra et al. 2020</th>
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<td><em>S. danae</em> (Sulzer, 1776)</td>
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<td><em>S. striolatum</em> (Charpentier, 1840)</td>
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<td><em>S. nigrifemur</em> (Selys, 1884)</td>
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<td><em>S. depressiusculum</em> (Selys, 1841)</td>
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<td><em>S. vulgatum</em> (Linnaeus, 1758)</td>
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<td><em>S. meridionale</em> (Séllys, 1841)</td>
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<td><em>S. sinaiticum</em> Dumont, 1977</td>
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<td><em>S. tibiale</em> (Ris, 1897)</td>
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<td><em>S. ibericum</em> (Spain)</td>
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<td><em>S. haritonovi</em> Borisov, 1983</td>
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drawing-person or to the individual variability (of the drawn specimen). Inside this group, three patterns of the hamular processes can be distinguished:

- internal (anterior) process shorter than the posterior: *S. fonscolombii*, *S. flaveolum*, *S. depressiusculum*, *S. vulgatum*
- internal process longer than the exterior one: *S. pedemontanum*, *S. striolatum*
- internal and external processes nearly equal: *S. meridionale*, *S. sanguineum*, *S. danae*.

The broad and rhomboidal shape of the outer hamular process is particular in *S. fonscolombii*, *S. flaveolum*, *S. pedemontanum*.

The relevance of these patterns for phylogenetic analyses and species delimitation is unknown.

With respect to the vulvar scale, the terminology used in the literature for the shape of its posterior edge (the apex, the distal or the apical edge) varies and must be presented first:

- bilobed / not bilobed, weakly bilobed (for *decoloratum*), two widely-separated lobes (for *fonscolombii*), two quite closely-approximated points (for *flaveolum*), with a small apical incision (for *pedemontanum*) (Askew 2004)
- with a small incision = incised (for *pedemontanum*), pointed (for *sanguineum*), with 2 distinct points or a double pointed vulvar scale (for *flaveolum*), with broad U-shaped incision (for *fonscolombii*) (Dijkstra et al. 2020)

The shape of the distal part of the vulvar scale in *Sympetrum* species show an exceptional variability, illustrated but not always described in words by authors. Within this variability, 2 distinct patterns can be distinguished:

a) clearly bilobed, no matter of the degree of lobation (large or weakly bilobed) or of the size of the lobes (pointed, incised): *fonscolombii*, *flaveolum*, *pedemontanum*, *striolatum*, *meridionale*

b) not bilobed, with the apical (distal) edge straight (not bilobed) or/and largely rounded: *vulgatum*, *danae*

Between these two patterns, particular distal edges of the vulvar scale are found in:

- *S. depressiusculum* – straight with a central lamina
- *S. meridionale* – largely and weakly bilobed with a sort of superposed central lamina
- *S. sanguineum* – a large variability in various authors descriptions.

**The subjectivity in establishing the taxonomic level / rank entities (species or subspecies) within group G.I.**

Describing and naming a species around the years 1800 is one thing but establishing the taxonomic rank of much more numerous entities after the years 2000 it has a certain difficulty. A hypothetic example would be that of 3 species with overlapped geographical ranges (sympatric) and with very similar (but not identical) vulvar scales and hamules. The interpretation of the taxonomic rank may be different:

i) the 3 “species” can be considered as only one species with a certain degree of variability, maybe subspecies or ii) good, distinct species reproductively isolated at only one level or at serially 2 – 3 – or more levels (morphology, phenology, reproductive behaviour, flight pattern). In such case their phenologies should not overlap, and phenology can be influenced by climate. The reproductive biology and the general biology of the three morphological entities must be very well known to declare a true reproductive isolation.

In the specific case of *S. sanguineum* the varying aspects of the vulvar scale (straight, appointed, bifid) may/can be seen as part of intraspecific variability only if the hamular processes also fall into the intraspecific variability. The question “Only one species with dimorphic females or two sibling species with identical males?” is legitimate too. In our case,
the females with different vulvar scale might be assigned to *S. sanguineum*; they may be part of a distinct population, different than others (a kind of inter-populational variability).

In the specific case of *S. meridionale* of this paper (from Cilieni), the bifid aspect of the vulvar scale should be analysed in relation with the hamules presented in the literature. The literature presents an insufficient description and a kind of degree of variability of the hamular processes: the hamules has long processes (Askew 2004); internal processes equal to external processes, raised much higher and bent at the apex (Cîrdei & Bulimar 1965), Dijkstra et al. 2020. Compared with the literature, the hamules of *meridionale* of this paper show **small critical** differences: their identity with *meridionale* cannot be confirmed. The interpretation of this Cilieni population:
- strictly and only with respect to the hamular processes it may be interpreted as i) intraspecific variability of *meridionale* or ii) on the reason that if on small critical differences *nigrescens* and *nigrifemur* are good species in the *striolatum* complex, then, on the same small critical differences, the Cilieni population can be considered a distinct species in a *meridionale* complex.
- considering the other two elements – the vulvar scale and the colour of the legs, the Cilieni population may be seen as a distinct morphological entity with a taxonomic rank (good species) or just a distinct population with different morpho-characters (inter-populational variability).

**The G.II. group**

*S. nigrifemur* and *S. nigrescens* are closely related with *S. striolatum* and together they form the *S. striolatum* group (Askew 2004). On the structure of the genitalia brought by Gardner, Askew (2004) considers *S. nigrescens* “a good species and not just a melanistic form of *S. striolatum*. Nevertheless, Askew (2004) takes the matter “still not firmly resolved”. *S. nigrifemur* is also considered a good species by Askew (2004) based on genital characters brought by Gardner.

Morphology of the genitalia corroborated with the geo-range allow the following interpretations:
- *S. nigrifemur* (Madeira and the Canaries) is geographically isolated by *S. striolatum* and their genitals are not identical, thus, *nigrifemur* may be seen as a good species. But the great similarity between *nigrifemur* and *striolatum* of both vulvar scale and hamules allows the subjective interpretation that *nigrifemur* is just at most a subspecies of *striolatum*, if not just a population extending the *S. striolatum* geo-range.
- *nigrescens* and *striolatum* may/might be good sympatric species. Although the geo-range of *S. nigrescens* is limited and overlapped with the margin of *S. striolatum* areal, the genitalia structures and especially the hamular processes differ, with respect to the shape and the length of the outer hamular process, as figured in the literature.
- *nigrescens* and *nigrifemur* can as well be considered distinct populations candidate for species formation.

**Sympetrum decoloratum**

Askew (2004) considers *S. decoloratum* a good species adapted to desert conditions. Askew (2004) put *S. decoloratum* in relation with *S. striolatum* by the vulvar scale and with *S. depressiusculum* by the male accessory genitalia. The status of good species is given by Askew (2004) on the distinctiveness of the abdominal appendages, according to Barteneff.

Dijkstra et al. (2020) considers *decoloratum* a subspecies of *S. vulgatum*. 
The geo-range of *decoloratum* is small – Asia Minor, Caucasus, Iraq, Pakistan, N. Africa (Libia, Tunisia, Algeria) (Askew 2004). Compared to the species related with, the geographical range of *decoloratum* is restricted in the southern part of *S. vulgatum*, *S. striolatum* and *S. depressiusculum*. It might overlap very little with *S. striolatum*, but not with *S. vulgatum* and *S. depressiusculum*. The rank of *decoloratum*, with a limited range at the margin of another species should be that of a subspecies or a distinct populations candidate for species formation.

The problem of areal is one of a major importance in zoogeography and in inferring the speciation patterns. Bănărescu (1970), quotes de Lattin who gives the definition of the areal: “the territory where the species reproduces regularly, without input from outside”. Thus, there is a nuanced difference between areal and geographical range, especially in the case of Odonata, insects with excellent flying abilities.

The speciation mechanisms are unknown in Sympetrum.

Bănărescu (1973) makes a clear distinction between *speciation* and *evolution* of a species. *Speciation* is defined as species formation (the German word Artbildung is very suggestive). 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. *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 populations with variable characters (for instance the Sympetrum populations with females with atypical bifid vulvar scale) may be part of a speciation mechanism or of a species evolution in time. This comes in agreement with Tennessens (1982) concluding remark: “behavioral and morphological characteristics, some of which are important in isolating species often vary amongst populations within the geographic range of species”.

Bănărescu (1973) considers that possibility of sympatric speciation in biparental organisms is doubtful 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.

Finally, some aspects of interspecific hybridization:

Occasional hybridization occurs between sympatric species, but the natural occasional interspecific hybrids are very rare – 1 hybrid individual: 60 000 specimens in birds, 6 hybrids: 100 000 specimens in mammals, 1 hybrid: thousands of specimens in Strongylocentrotus (Bănărescu 1973). As previously expressed in this paper, Sympetrum species were reported to have produced hybrid individuals (Tennessen 1982) but their percentual frequency in nature (not laboratory hybrids) is not documented. Sánchez-Guillén et al. (2013-2014) give a new perspective of genetic methods in predicting reproductive isolation in Odonata.
Bănărescu (1973), citing Mayr (1963) presents 3 types of interspecific hybridization with importance in 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. It is viewed possible between *vulgatum* and *decoloratum* by Hinojosa et al. (2017). The outcome is the incorporation into the gene pool of a species, of genes that belonged to another species.
- **mass hybridization** between sympatric species with the emergence of a hybrid swarm or a hybrid population
- **species formation (speciation)** through hybridization followed by alloploidy

These aspects are very little documented for Sympetrum.

The nine Sympetrum European species with a large geographical range were described and named between 1758 and 1841 based on morphology alone, most probably on a very small number of specimens, in a time when matters as type specimens and species concepts were unknown. From then until now, zoologists considered the species named in the years 1700-1800 to be good species and we are currently seeking to discover how they are reproductively isolated.

Another facet of the Sympetrum problem could be the existence of far fewer than nine species, evolving in time. Surely, we cannot speak about only one Sympetrum species evolving in time – climate change during geological era has led to “the fragmentation of populations” and thus, led to speciation (Hinojosa et al. 2017).

**Conclusions**
1) The genus Sympetrum prove to be a genus with an exceptional morphological variability. 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? Is it at least in some cases controlled at the epigenetic level? the characters stability in space and time,
2) The mechanisms of reproductive isolation of Sympetrum species are not clearly known. The speciation mechanisms are unknown.
3) The heterospecific pairing, the occasional hybridization and the great morphological variability suggest un incomplete / inefficient species reproductive isolation.
4) There are too many gaps in the Sympetrum knowledge for an impeccable, flawless judgement and until answers will come, we can speculate: because of sympatry and lack of perfect reproductive isolation, speciation it is not or cannot be completed. At a large scale, some of the species might be just populations of an only one species evolving in time; others might be populations candidate for becoming species, or incipient species, or good species, and gene-flow between all these types.

**References**


Babalean A. F., 2022, *Sympetrum sanguineum* Newman, 1833 (Odonata, Anisoptera) - only one species with dimorphic females or two sibling species with identical males?, [https://doi.org/10.1101/2022.09.17.508356](https://doi.org/10.1101/2022.09.17.508356)

Babalean A. F., 2022, Contribution to the genus Sympetrum Newman 1833 (Odonata, Anisoptera) from extreme S-W Romania, [https://doi.org/10.1101/2022.10.31.514645](https://doi.org/10.1101/2022.10.31.514645)


August 03 2023