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On the natural interspecific hybrids of *Ophrys mammosa* Desf. s. l. and *O. oestrifera* M. Bieb. (Orchidaceae) from the Crimea and the North Caucasus

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Summary. Two natural interspecific hybrids of *Ophrys mammosa* Desf. s. l. and *O. oestrifera* M. Bieb. (*O.* × *aghemanii* Renz) are reported from Russia: a very rare *O. mammosa* subsp. *mammosa* × *O. oestrifera* from the Crimea (vicinity of Zelenogorye) and a relatively abundant *O. mammosa* subsp. *caucasica* (Woronow ex Grossh.) Soó × *O. oestrifera* from the Krasnodar Territory (vicinity of Bolshoy Utrish). Males of *Andrena carantonica* Pérez are recorded as efficient pollinators of apparently both *O. mammosa* subsp. *caucasica* and *O. oestrifera* at the site where their hybrids occur.

О естественных межвидовых гибридах *Ophrys mammosa* Desf. s. l. и *O. oestrifera* M. Bieb. (Orchidaceae) в Крыму и на Северном Кавказе

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Ключевые слова: интрогрессия, опылитель, офрисы, Россия, *Andrena carantonica*, *Ophrys* × *aghemanii*, *Ophrys scolopax* s. l., *Ophrys sphegodes* s. l.

Аннотация. Для флоры России приведены два естественных межвидовых гибрида *Ophrys mammosa* Desf. s. l. и *O. oestrifera* M. Bieb. (*O.* × *aghemanii* Renz): очень редкий *O. mammosa* subsp. *mammosa* × *O. oestrifera* из Крыма (окр. с. Зеленогорье) и относительно обильный *O. mammosa* subsp. *caucasica* (Woronow ex Grossh.) Soó × *O. oestrifera* из Краснодарского края (окр. с. Большой Утриш). Самцы *Andrena carantonica* Pérez зарегистрированы на участке произрастания гибридов *O. mammosa* subsp. *caucasica* и *O. oestrifera* как эффективные опылители, вероятно, обоих видов.

Introduction

Taxonomy of the genus *Ophrys* L. is controversial and depends on the species concept adopted by the researchers. Ethologically oriented taxonomists recognize more than 350 species (so called microspecies) on the basis of intuited morphological differences and claimed pollinator specificity (Vereecken et al., 2011; Delforge, 2016; Paulus, 2018; Baguette et al., 2020). Genetically oriented orchidologists accept only nine *Ophrys* species (so called macrospecies) which are monophyletic entities that can be confidently identified through candidate gene sequencing of a few well-chosen, readily analyzed genic regions, as well as using morphology, by even inexperienced field botanists (Devey et al., 2008; Bateman et al., 2011, 2018, 2021). Some other authors (e. g., Véla et al., 2015; Fateryga et al., 2018) propose to recognize ca. 30–80 species which can be circumscribed on the base of traditional morphology without taking into account the genetics (so called mesospecies or morphospecies). The mesospecies are clearly categories of convenience, but unlike the microspecies and macrospecies, it is believed that there is no particular underlying species concept available to justify their recognition (Bateman et al., 2021).

There are four species of the genus *Ophrys* in Russia; they were recently revised taxonomically according to the mesospecies approach (Fateryga et al., 2018; Efimov, 2020). Each of them, however, belongs to a separate macrospecies. These species are *Ophrys apifera* Huds. (macrospecies *O. apifera*), *O. insectifera* L. (macrospecies *O. insectifera*), *O. mammosa* Desf. (≡ *O. sphegodes* subsp. *mammosa* (Desf.) Soó ex E. Nelson; macrospecies *O. sphegodes* Mill.), and *O. oestrifera* M. Bieb. (= *O. scolopax* subsp. *cornuta* (Steven) E. G. Camus; macrospecies *O. fuciflora* (F. W. Schmidt) Mönch). *Ophrys insectifera* is distributed through the European part of Russia (excluding the Crimea and the North Caucasus) and Urals while three other species are conversely present only in the Crimea and the North Caucasus (Fateryga et al., 2018; Efimov, 2020). *Ophrys mammosa* is the most polymorphic species in Russia, with two formally recognized

subspecies: *O. mammosa* subsp. *mammosa* from the Crimea and the Republic of Dagestan and *O. mammosa* subsp. *caucasica* (Woronow ex Grossh.) Soó (≡ *O. sphegodes* subsp. *caucasica* (Woronow ex Grossh.) Soó) from the Krasnodar Territory. The latter taxon may supposedly have an introgressive origin due to its characters somewhat intermediate between typical *O. mammosa* and *O. oestrifera* (Fateryga et al., 2018). A recent phylogenetic study (Bateman et al., 2021) revealed that *O. mammosa*, as a mesospecies, was polyphyletic in relation to other mesospecies within the *O. sphegodes* macrospecies; *O. mammosa* subsp. *caucasica* was not included to that analysis.

Besides the four well recognized species and one putative subspecies, a natural interspecific hybrid of *O. apifera* and *O. oestrifera* is known as *O. × val-lis-costae* Kümpel from both the Crimea and the North Caucasus (Fateryga et al., 2018). Although H. F. Paulus (2018: 262) believes that hybrids in the genus *Ophrys* are “only frequent in literature and not in nature”, the genetic data show considerable gene-flow even among the nine macrospecies (see Bateman, 2018). Therefore, other hybrids were also expected to be found in the Crimea and the North Caucasus in the localities where more than one species of the genus occur. Such hybrids were, however, not registered during a short two-year period (2016–2017) of the previous field studies (Fateryga et al., 2018). Further observations revealed the presence of hybrids of *O. mammosa* subsp. *caucasica* and *O. oestrifera* in four localities in the Krasnodar Territory (Popovich et al., 2020); though, they were not documented by specimen-based records and no detailed information was provided.

The purpose of the present contribution is to report the hybrids of *O. mammosa* s. l. (including *O. mammosa* subsp. *caucasica*) and *O. oestrifera* from both the Crimea and the North Caucasus.

Material and methods

Living plants were observed in the Crimea and the Krasnodar Territory in 2020–2021. The presence of hybrids as well as their parent species was documented with digital cameras. A leaf and a

few flowers were collected from one or two hybrid plant in each locality. Supposed pollinators (males of solitary bees) were sampled around the sites with flowering *Ophrys* plants using an entomological net during at least three hours with a sunny weather in each site. The bees were identified according to C. Schmid-Egger and E. Scheuchl (1997) and E. Scheuchl (2006); their names were accepted according to the “Annotated catalogue of the Hymenoptera of Russia” (Antropov et al., 2017).

Results and discussion

Ophrys mammosa Desf. subsp. *mammosa* × *O. oestriifera* M. Bieb. (Fig. 1C–F)

Specimens examined: “Crimea, vicinity of Zelenogorye, Pananyan-Uzen River valley, 44°53'01"N, 34°42'31"E [ca. 390 m. a. s. l.], rocky slope to river, among shrubs. 28 V 2020. A. V. Fateryga s. n.” (PHEO).

Notes: The *Ophrys* spp. plants were found on an open slope next to a river, near a waterfall (Fig. 1A). A single group of three hybrid specimens in flower was registered in both 2020 and 2021 (Fig. 1C). Parent species (Fig. 1B, G) were represented by more than a hundred flowering individuals each. Hybrid plants started to flower in mid-May, after most specimens of *O. mammosa* but far before the earliest specimens of *O. oestriifera*.

Bee collecting at the site with the hybrids on 15 V 2021 revealed only a male specimen of *Megachile* (*Chalicodoma*) *parietina* (Geoffroy) bearing pollinaria but of *Anacamptis morio* subsp. *caucasica* (K. Koch) H. Kretzschmar, Eccarius et H. Dietr., not of any *Ophrys* species. *Ophrys mammosa* is claimed to be pollinated exclusively by *Andrena* (*Melandrena*) *morio* (Brullé) (Paulus, 2018), but the only known pollinator collected hitherto in the Crimea was a single male of *Eucera* (*Eucera*) *longicornis* (L.) (Kreutz et al., 2018; Fateryga et al., 2019). It is well known that *O. oestriifera* is pollinated by various species in the genus *Eucera* Scop., including *E. longicornis* (Claessens, Kleynen, 2011; Kreutz et al., 2018; Fateryga et al., 2019). Therefore, it is highly possible that the hybrid plants originated from a cross-pollination event performed by such a mutual pollinator as *E. longicornis*. The rarity of this hybrid in the Crimea can be explained by a very low general pollination rate of both parent species, the lowest among all deceptive orchids occurring there (Kreutz et al., 2018).

The name *Ophrys* × *aghemanii* Renz should be applied to all the hybrids of *O. mammosa* and

O. oestriifera. The type specimen of *O. × aghemanii* form Iran (RENZ 10842, URL: <https://orchid.unibas.ch/index.php/en/database-search/advanced-search?SearchResultID=10842>) is, however, labeled with another hybrid formula: *O. scolopax* Cav. × *O. turcomanica* Renz. Typical *O. scolopax* is distributed in the West Mediterranean while it is replaced by *O. oestriifera* (= *O. scolopax* subsp. *cornuta*) in Iran; as for *O. turcomanica*, it is treated as a synonym of *O. mammosa* (≡ *O. sphegodes* subsp. *mammosa*) (Govaerts et al., 2005–2022; Fateryga et al., 2018). Thus, there is no doubt that J. Renz described a hybrid of *O. mammosa* and *O. oestriifera* in their current treatment.

Ophrys mammosa subsp. *caucasica* (Woronow ex Grossh.) Soó × *O. oestriifera* M. Bieb. (Fig. 2C–F)

Specimens examined: “Krasnodar Territory, Anapa Urban Okrug, vicinity of Bolshoy Utrish, 44°45'29"N, 37°23'53"E [ca. 85 m a. s. l.], juniper forest. 3 V 2021. A. V. Fateryga, A. V. Popovich, s. n.” (PHEO).

Notes: The plants were found on an open mountain slope in a Greek juniper sparse forest (Fig. 2A). There were 34 hybrid specimens along with 32 specimens of rather pure *O. mammosa* subsp. *caucasica* and 33 specimens of *O. oestriifera* (calculated in 2021). Hybrid plants had various flower shape and color pattern (cf. Fig. 2D, E), often more similar to either parent species (Fig. 2B, G). In both 2020 and 2021, hybrids started to flower in late April, approximately simultaneously with most specimens of *O. mammosa* subsp. *caucasica* but before most specimens of *O. oestriifera*.

Bee collecting at the site with the hybrids on 3 V 2021 resulted in 13 males of *Andrena* (*Hoplandrena*) *carantonica* Pérez (= *A. jacobi* Perkins) and two males of *Osmia* (*Osmia*) *bicornis* (L.). Ten males of *A. carantonica* were with *Ophrys* pollinaria attached to the clypeus (Fig. 3). It was impossible to ascertain of what *Ophrys* species these pollinaria were (examination of pollinaria taken from flowers of both species revealed that they had no visible differences). The number of pollinaria born by an *A. carantonica* male were five, three (in one specimen each), two (in five specimens), and one (in three specimens). Most pollinaria were incomplete, with a part of the massulae had been already spent (apparently to fertilize flowers), or even represented by the caudicula (in three cases) or the viscidium only (in one case). This meant that the collected males of *A. carantonica* apparently was not occasional visitors of the

flowers (“pollinaria thieves”, see Paulus, 2018) but took a valuable part in the pollination process. The presence of efficient pollinators in a sufficient density may explain a high proportion of hybrid plants of *O. mammosa* subsp. *caucasica* and *O. oestrifera* in the vicinity of Bolshoy Utrish, especially in compar-

ison with the hybrids of *O. mammosa* subsp. *mammosa* and *O. oestrifera* in the Crimea. Therefore, it is also not surprising that the hybrid of *O. mammosa* subsp. *caucasica* and *O. oestrifera* was reported from several localities in the Krasnodar Territory (Popovich et al., 2020).

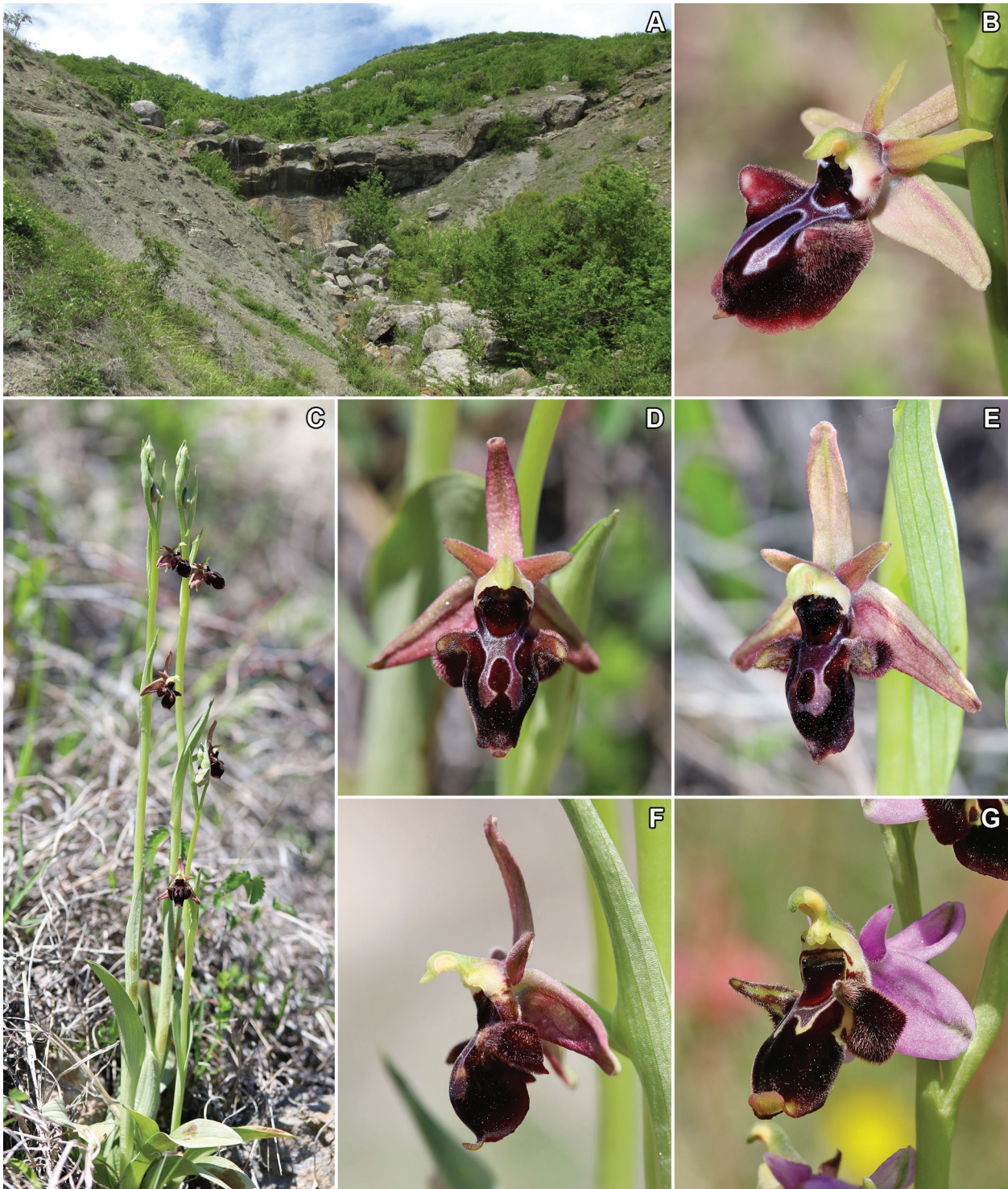


Fig. 1. *Ophrys* spp. in the vicinity of Zelenogorye (Crimea): A – habitat; B – flower of *O. mammosa* Desf. subsp. *mammosa*; C–F – *O. mammosa* subsp. *mammosa* × *O. oestrifera* M. Bieb. (C – habit of plants in flower; D–F – flowers); G – flower of *O. oestrifera*. Photos by A. V. Fateryga.



Fig. 2. *Ophrys* spp. in the vicinity of Bolshoy Utrish (Krasnodar Territory): A – habitat; B – flower of *O. mammosa* subsp. *caucasica* (Woronow ex Grossh.) Soó; C–F – *O. mammosa* subsp. *caucasica* × *O. oestrifera* M. Bieb. (C – habit of a plant in flower; D–F – flowers); G – flower of *O. oestrifera*. Photos by A. V. Fateryga.

The hybrid between *O. mammosa* subsp. *caucasica* and *O. oestrifera* is not formally described as a nothosubspecies. The phylogenetic position of *O. mammosa* subsp. *caucasica* was not studied by R. M. Bateman et al. (2021), and it may be possible that this putative subspecies itself has a hybridogenous origin (cf. Fateryga et al., 2018). It is to note

that if the macrospecies concept will be accepted (with *O. mammosa* being merged into *O. sphegodes* and *O. oestrifera* being merged into *O. fuciflora*), the names of all possible interspecific hybrids in the genus *Ophrys* appear to be already available (Bateman et al., 2018, 2021).

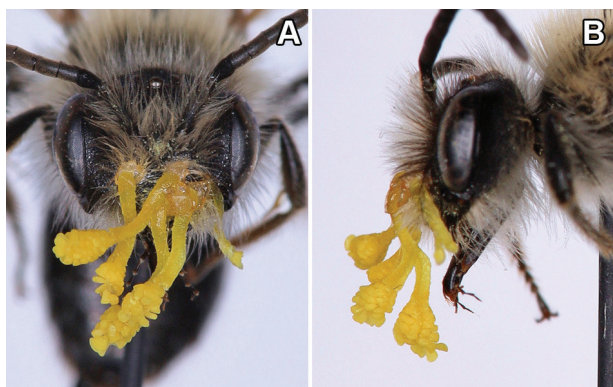


Fig. 3. Head of an *Andrena carantonica* Pérez male with *Ophrys* spp. pollinaria: A – frontal view; B – lateral view. Photos by A. V. Fateryga.

Conclusions

Natural interspecific hybrids of *O. mammosa* s. l. and *O. oestrifera* (*O.* × *aghemanii* s. l.) are reported from the Crimea (for the first time) and the Krasnodar Territory. These hybrids very rarely

occur in the Crimea where the pollination rate of both parent species is very low. The proportion of the hybrid plants is high in the vicinity of Bolshoy Utrish in the Krasnodar Territory (about a third of all *Ophrys* individuals) where a sufficient density of the efficient pollinators is recorded.

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