

# About the recent transfer of the species-group taxon *floccifera* and its closest relatives from the genus *Carcharodus* to the genus *Muschampia* (Lepidoptera: Hesperidae, Pyrginae)

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**Abstract.** The taxonomic history of skippers usually placed in the genus *Carcharodus* is surveyed, and the recent transfer to the genus *Muschampia* of the species-group taxon *C. floccifera* and its closest relatives (apart from *C. alceae* and *C. tripolina*) is discussed and questioned on the basis of extensive genitalia character differences detected in both sexes between *C. floccifera* and its kin, and *M. proto* (= type species of the genus *Muschampia*).

**Samenvatting.** De taxonomische geschiedenis van dagvlinders die gewoonlijk in het genus *Carcharodus* worden geplaatst, wordt onderzocht en de recente overdracht naar het genus *Muschampia* van het soortgroep taxon *floccifera* en zijn naaste verwanten (behalve *C. alceae* en *C. tripolina*) wordt besproken en bestudeerd op basis van uitgebreide informatie van verschillen in de genitalia bij beide geslachten tussen de laatste en zijn verwanten, en *M. proto* (= typesoort van het genus *Muschampia*).

**Résumé.** L'histoire taxonomique des Hespéries habituellement placés dans le genre *Carcharodus* est étudiée et le transfert récent au genre *Muschampia* du groupe d'espèces de *floccifera* et de ses plus proches parents (autres que *C. alceae* et *C. tripolina*) est discuté et remis en question sur la base de différences de génitalia détectées chez les deux sexes entre ce dernier et ses parents, et *M. proto* (= espèce type du genre *Muschampia*).

**Key words:** *Carcharodus* – genitalia – Hesperidae —mt-DNA barcoding — *Muschampia proto* — *Reverdinus floccifera*.

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## Introduction

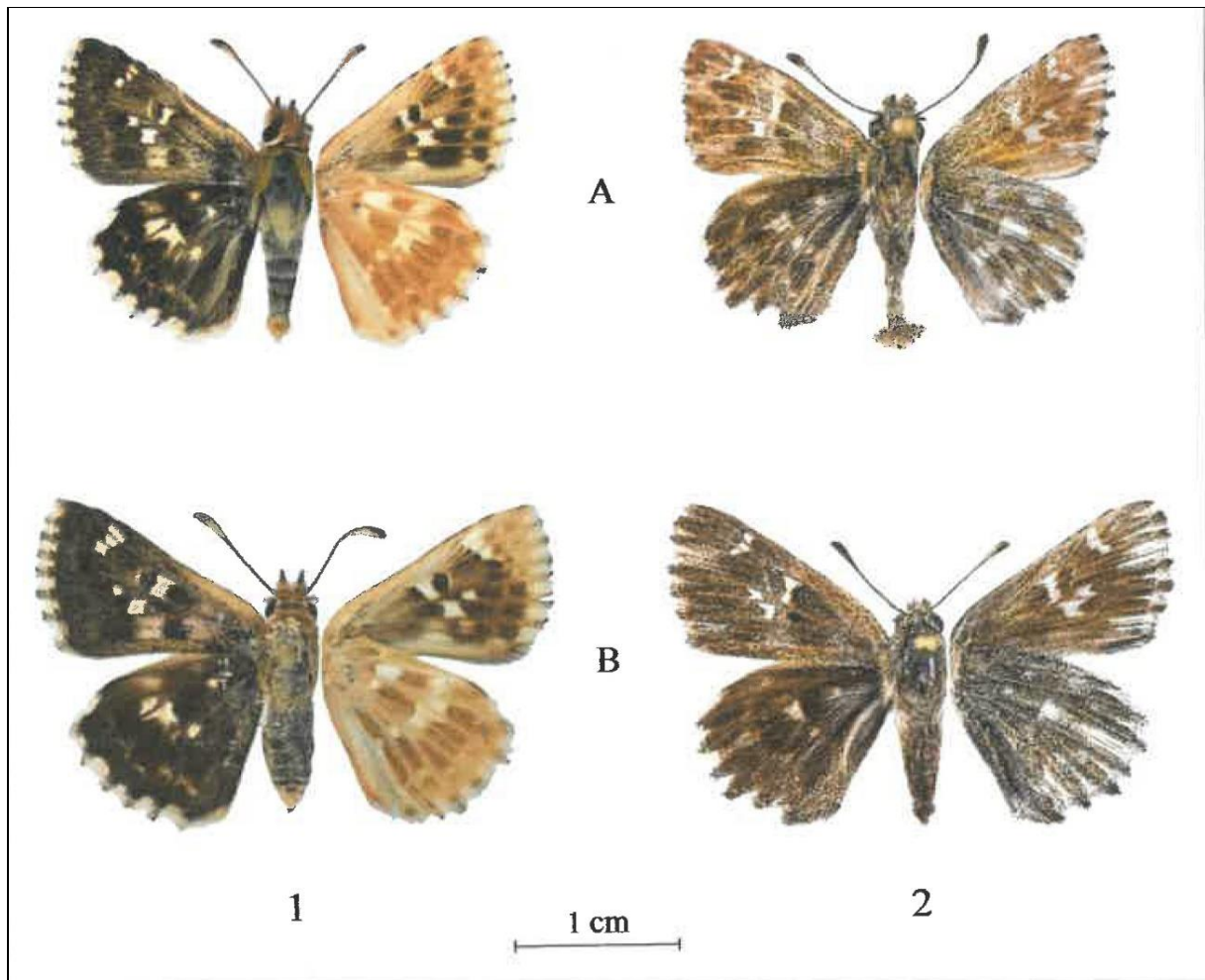
With the exception of *Carcharodus alceae* (Esper, [1780]) and *C. tripolina* Verity, 1925, both of which in more recent times have shown signs of generic stability, the remainder of the members in the group have shown for various reasons a rather peripatetic disposition, moving in and out of *Carcharodus* Hübner, [1819], entering and leaving genera such as *Reverdinus* Ragusa, 1919, and *Lavatheria* Verity, 1940, and all currently having been placed in *Muschampia* Tutt, [1906], a very unexpected rearrangement.

By the middle of the second decade of the 20<sup>th</sup> century, the genus *Carcharodus* contained in chronological order the following species: *C. alceae*, *C. baeticus* (Rambur, 1839), *C. floccifera* (Zeller, 1847), *C. dravira* (Moore, [1875]), *C. orientalis* Reverdin, 1913 and *C. stauderi* Reverdin, 1913. In 1919, Ragusa created the new genus *Reverdinus* (type species: *Papilio altheae* Hübner, [1800–1803] = *Hesperia floccifera* Zeller, 1847) in order to separate generically the untufted FW underside *alceae* from the tufted *floccifera* and its closest relatives. This action, however, had little appeal and was followed much later by very few authorities, including Verity (1940) and Forster & Wohlfahrt (1976). Verity used his experience in butterfly genitalia to describe in 1925 *C. tripolina*, to verify even further which species other than *floccifera* belonged to *Reverdinus* and to decide what to make of the taxon *lavatherae*, the male genitalia of which did not fit well in either *Carcharodus* or *Reverdinus*. He decided to place it in a new genus *Lavatheria* (type species: *Papilio lavatherae* Esper, [1783]), a move which has been practically ignored by all, along with the

continuing lack of acceptance of *Reverdinus*. Higgins (1975), who was well aware of genital differences in the group, wrote the following in respect of *Reverdinus* and *Lavatheria*: “Ragusa (1919) proposed a new genus *Reverdinus* for this species [i.e., *floccifera*]. It does not appear to the author that generic distinction is necessary.” and “Verity (1940) proposed a new genus *Lavatheria* for this species [i.e., *lavatherae*], but it does not appear to the writer that generic distinction is required.” It is strange that Higgins, who often either accepted or created new genera on the basis of genital minutia (e.g., *Mellicta* Billberg, 1820, *Hypodryas* Higgins, 1978, *Eurodryas* Higgins, 1978), should be so strict in cases in which genital differences appear to be greater in both number as well as extent.

About a hundred or so years have passed since the second decade of the 20<sup>th</sup> Century, when the six aforementioned species were placed in *Carcharodus*, and despite all previous attempts at changes on the generic level, the genus remained the same, with the addition of *C. tripolina*.

In 2016 (*a* & *b*), Coutsis proposed a new taxonomic revision of the group, based on features of both male and female genitalia. It was found that the genitalia of *C. alceae* and *C. tripolina* differed substantially in many respects from those of *C. floccifera* and its related species, and that those of *C. lavatherae*, though not identical, resembled those of *C. floccifera* and its closest relatives. It was therefore proposed to retain the taxa *alceae* and *tripolina* in *Carcharodus*, to reinstate *baeticus*, *floccifera*, *dravira*, *orientalis* and *stauderi* in *Reverdinus*, and finally to place *lavatherae* in *Lavatheria*, treated as a subgenus within *Reverdinus*.



**Plate 1.** Adults.

**Fig. 1.** *Muschampia proto* (Ochsenheimer, 1808). A. Male, ex ovo found on *Phlomis* sp. 8.iv.2018. Greece, Pelopónnisos, Leonídhio, adult hatched 26.vi.2018, reared D. Benyamini. B. Female, same data as for male.

**Fig. 2.** *Reverdinus floccifera* (Zeller, 1847). A. Male, spec. No. 24526/7, Italy, Sicily, Rocca Busambra (about 30 km S. of Palermo), Palermo, 1100 m, 13.v.2006, leg. E. Punta, in coll. M. Albrecht. B. Female, spec. No. 24529/9, Italy, Gole de Gouta, Imperia, 1200 m, 22.vi.2006, leg. E. Punta, in coll. M. Albrecht.

As far as we know, all these proposals have likewise been ignored. It is of interest to observe here that the male genitalia of *alceae* and *tripolina* were found to have more in common with those of some species presently placed in *Muschampia* than with those of *floccifera* and its close relatives.

In 2020, Zhang *et al.* produced a revisionary paper on the subtribe Carcharodina as a whole, based on mt-DNA barcoding. They came to the conclusion that *alceae* and *tripolina* should remain in *Carcharodus* and that all the other taxa in the group should be moved out of it, thus agreeing in these two respects with Coutsis (2016a & b). However, whereas Coutsis transferred the remaining taxa to *Reverdinus*, Zhang *et al.* placed them in *Muschampia*, a poorly defined genus, the type species of which, *Papilio proto* Esper, [1805–1808] is very different from the *floccifera* group in both external and genitalic characters. This transfer was accepted, but with some reserve, by Benyamini & John (2020), before any detailed comparative study between the female genitalia of *proto* and those of *floccifera* and its close relatives became available.

The present authors find the decision questionable. The purpose of this paper is to show in detail the many,

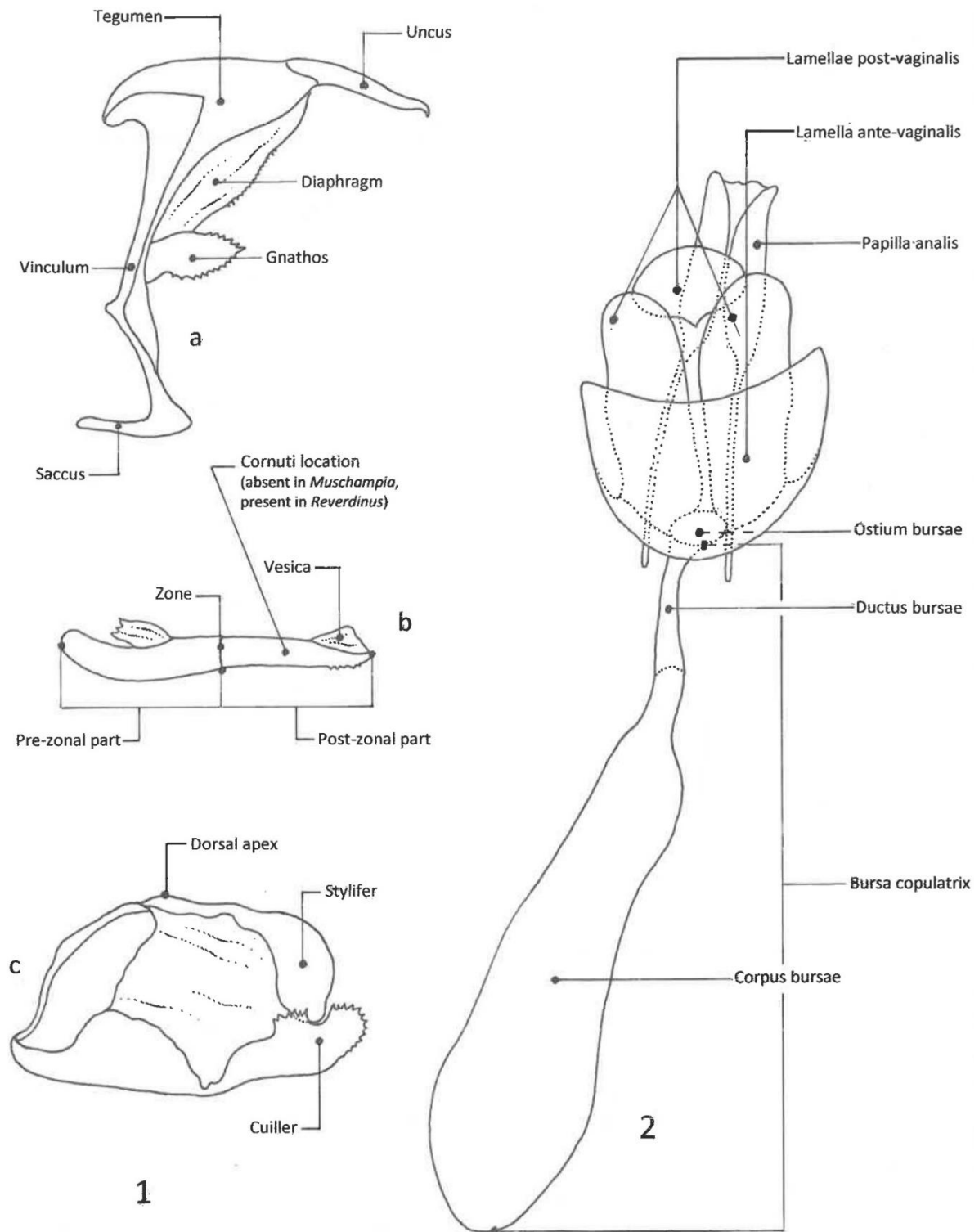
diverse and often pronounced differences in both male and female genitalia between *M. proto* ((Pl. 1, Figs 1A–B) and *R. floccifera* ((Pl. 1, Figs 2A–B), respectively type species of *Muschampia* and *Reverdinus*) and to express some doubt about the validity of placing *floccifera* and its close relatives in the genus *Muschampia*.

### The male genitalia of *Muschampia proto*

(Pl. 2, Figs. 1a–c; Pl. 3, Figs 1a–c c)  
(The genitalia terminology follows Tuxen (1970) and Higgins (1975))

**Genital ring:** (Fig. 1a). Gnathos *present*; diaphragm directly beneath uncus *not forming* rigid, horizontal platform, but *having* densely set and minute spinelets in area right above gnathos; saccus *short*.

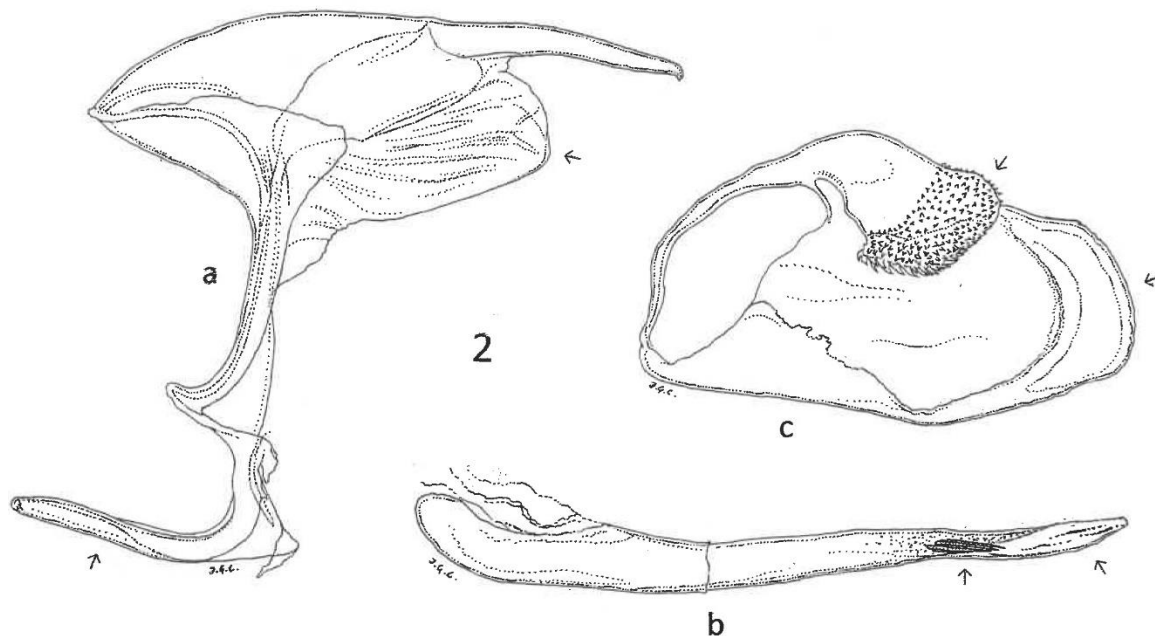
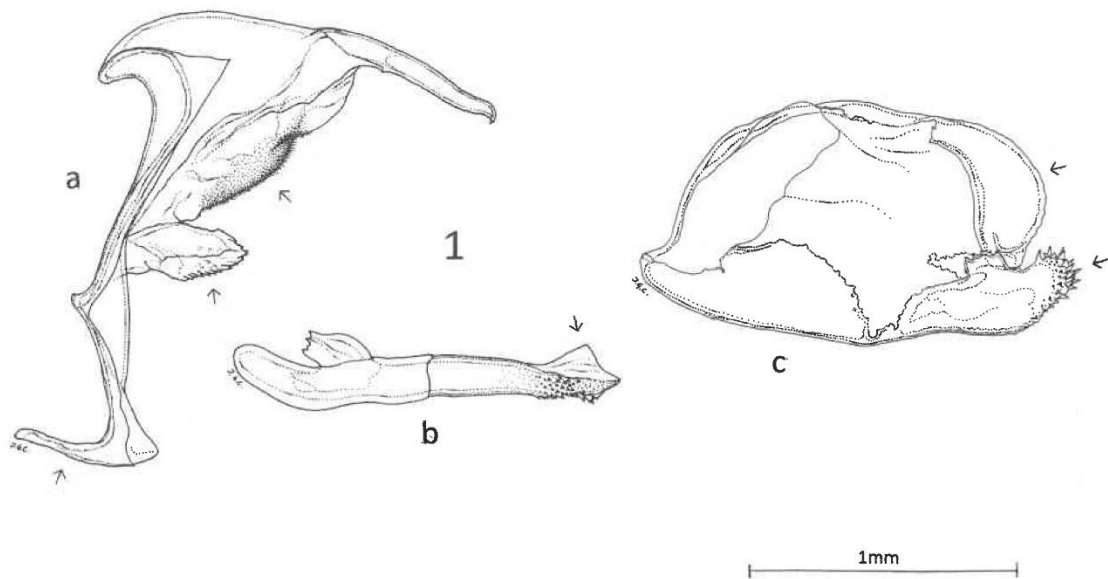
**Aedeagus:** (Fig. 1b). *Short* and slender; left side in lateral aspect with membranous vesica emerging from *dorsal side* of distal area of post-zonal part; interior *without* cornuti.



**Plate 2.** Explanatory drawings of genital appendages.

**Fig. 1.** Male *Muschampia proto* (Ochsenheimer, 1808). a. Lateral aspect of left side of genital ring. b. Lateral aspect of left side of aedeagus. c. Lateral aspect of inner face of right valva.

**Fig. 2.** Female *Reverdinus floccifera* (Zeller, 1847). Ventral aspect of bursa copulatrix together with the papillae analis and the lamellae ante- and post-vaginalis.



**Plate 3.** Male genital appendages.

**Fig. 1.** *Muschampia proto* (Ochsenheimer, 1808), Greece, Sími Island, Sími town, 50 m, 3.vi. 1993. Prep. No. 3031, leg. J. G. Coutsis.

**Fig. 2.** *Reverdinus floccifera* (Zeller, 1847), Greece, Makedhonía, Flórina Prefecture, near Písodhéri, ca 1400 m, 7.viii.1980. Prep. No. 1405, leg. J. G. Coutsis. a. Lateral aspect of left side of genital ring that includes the vinculum, tegumen, diaphragm, uncus, saccus and, when present, the gnathi. b. Lateral aspect of left side of aedeagus. c. Lateral aspect of inner face of right valva.

**Valva:** (Fig. 1c). Stylifer *narrow, long and smooth*, and extending distad *way beyond* dorsal apex of valva; cuiller dorso-distally *bilobed, carrying spines*, and not extending far above ventrum of valva.

### The male genitalia of *Reverdinus floccifera*

(Pl. 3, Figs 2a–c)

(Cited characters also valid for all other *Reverdinus* taxa)

**Genital ring:** (Fig. 2a). Gnathos absent; diaphragm right under uncus forming rigid, horizontal platform,

membranous throughout, and devoid of any spinelets; saccus very long.

**Aedeagus:** (Fig. 2b). Very long and slender; left side in lateral aspect with membranous vesica emerging from side and ventrum of distal area of post-zonal part; interior with cornuti.

**Valva:** (Fig. 2c). Stylifer short, wide, with swollen and rounded distal 1/2 densely spinose, and extending distad only a short distance beyond dorsal apex of valva; cuiller wide, squarish and smooth, and extending across width of valva.

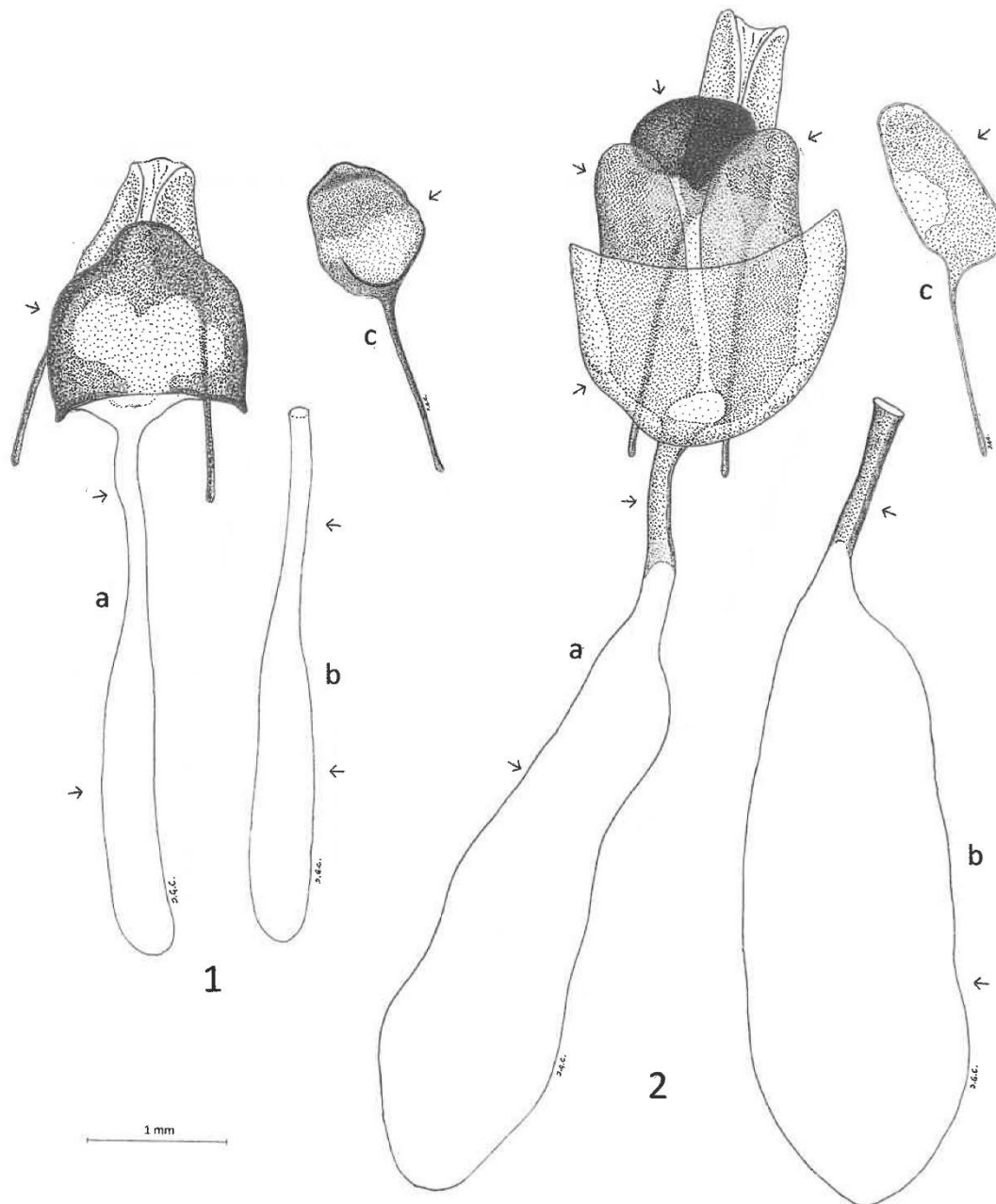


Plate 4. Female genital appendages.

**Fig. 1.** *Muschampia proto* (Ochsenheimer, 1808), Greece, Pelopónnisos, Mt. Panahaikó, 1300 m, 14.vii. 1989. Prep. No. 5989, leg. J. G. Coutsis.

**Fig. 2.** *Reverdinus floccifera* (Zeller, 1847), Greece, Makedhonia, Rodhópi Mts., Filákió Fraktú, 1400–1500 m, 11.vii.1993. Prep. No. 5992, leg. J. G. Coutsis.

**a.** Ventral aspect of bursa copulatrix together with the papillae analis and the lamellae in vicinity of the ostium bursae. **b.** Lateral aspect of left side of corpus bursae together with ductus bursae. **c.** Lateral aspect of exterior face of left papilla analis.

### The female genitalia of *Muschampia proto*

(Pl. 4, Figs 1a–c)

**Papillae analis:** in flat aspect rounded and short.

**Lamellae post-vaginalis:** absent.

**Lamella ante-vaginalis:** heavily sclerotized except centrally, wide at base and slender distally.

**Ostium bursae:** in ventral aspect at short distance from distal tips of papillae analis.

**Ductus bursae:** very long and entirely membranous.

**Corpus bursae:** fairly long; in both ventral and lateral aspects extremely slender.

### The female genitalia of *Reverdinus floccifera*

(Pl. 2, Fig. 2; Pl. 4, Figs 2a–c)

(Cited characters also valid for all other *Reverdinus* taxa)

**Papillae analis:** in flat aspect roughly elliptical, elongate.

**Lamellae post-vaginalis:** three are present, two of which in ventral aspect are elongate, quite heavily sclerotized and placed ventro-laterally, one on each side, the third one heart-shaped, very heavily sclerotized and placed ventro-centrally just distad of the two ventro-lateral ones.

**Lamella ante-vaginalis:** in ventral aspect very lightly sclerotized throughout, slender at base and wide distally.

**Ostium bursae:** in ventral aspect at long distance from distal tips of papillae analis.

**Ductus bursae:** fairly long and sclerotized.

**Corpus bursae:** very long; in ventral aspect fairly wide and in lateral one very wide and flask-shaped.

## Discussion

Structural differences between the genitalia of *M. proto* and *R. floccifera* relate to practically all genital components. There are differences, not only in the shape and size of components, but also by their presence or absence. In the male genital appendages differences exist in the shape and size of the aedeagus, the positioning of the vesica aperture, and the existence or not of cornuti; in the valve, the overall shape and proportions are different, as are also the shape, positioning and existence or not of spines on stylifer and cuiller; inside the genital ring there may or may not be a pair of gnathi, and the diaphragm may or may not have a rigid horizontal platform and an area of densely set spinelets. In the female genitalia there are differences relating to the size and shape of the papillae analis, the existence or not of lamellae post-vaginalis, the shape and surface texture of the lamella ante-vaginalis, the sclerotization or not of the ductus bursae and its length, the distance between the ostium bursae and the tip of the papillae analis, and finally the size and shape of the corpus bursae. All these differences taken together surely equal in number and importance those between the genitalia of *R. floccifera* and of taxa placed in either *Pyrgus* Hübner, [1819] or *Spialia* Swinhoe,

[1912], both of which are closely related to *Muschampia*, but otherwise fully accepted as separate genera.

In addition to all the above, it must also be borne in mind that the larval host-plant of *M. proto* is confined exclusively to *Phlomis* spp. (Benyamini & John 2020), while those of the majority of *Reverdinus* species are *Ballota*, *Marrubium* and *Stachys* spp. However, although the larvae of *R. stauderi* (Reverdin, 1913) normally feed on *Marrubium* and *Ballota*, in Egypt and the Sinai Peninsula in particular also feed on *Phlomis floccusa* and *P. aurea*.

## Conclusions

In our view, and on the basis of all the above, it seems to us more prudent to: a) retain *alceae* and *tripolina* in *Carcharodus* b) remove *floccifera* and its close relatives from *Carcharodus*, as already done by both Coutsis (2016a & b) and Zhang *et al.* (2020), and reinstate them in *Reverdinus*, subgenus *Reverdinus* and c) place *lavatherae* in *Reverdinus*, subgenus *Lavatheria*. We also believe that the discrepancies between our views and the mt-DNA results in Zhang *et al.* (2020), may eventually be resolved with the advent of a broader and deeper investigation into nucleus-DNA of butterflies.

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