

# The male and female genital structures of skippers currently placed in the genus *Carcharodus* Hübner, [1819] and their taxonomic significance (Lepidoptera: HesperIIDae, Pyrginae)

John G. Coutsis

**Abstract.** The male and female genitalia of skippers currently placed in the genus *Carcharodus* Hübner, [1819] are shown and described – some for the first time – and their taxonomic significance and implications are discussed in an attempt at re-defining the group's taxonomy and nomenclature.

**Samenvatting.** De mannelijk en vrouwelijke genitalia van de dikkopjes momenteel geplaatst in het genus *Carcharodus* Hübner, [1819] worden afgebeeld en beschreven, sommige voor de eerste maal. Hun betekenis voor de taxonomie en de implicaties daarvan worden besproken in een poging om de taxonomie en nomenclatuur van deze groep te herzien.

**Résumé.** Les genitalia mâle et femelle des espèces du genre *Carcharodus* Hübner, [1819] sont figurés et discutés, dont quelques-uns pour la première fois. Leur importance pour la taxonomie et les implications pour la systématique sont discutées dans une tentative de clarifier leur taxonomie et nomenclature.

**Key words:** Lepidoptera – HesperIIDae – Pyrginae – *Carcharodus* – *Reverdinus* – *Lavatheria* – *alceae* – *tripolina* – *floccifera* – *orientalis* – *dravira* – *baeticus* – *stauderi* – *lavatherae* – *Muschampia* – *poggei* – *proteus* – *staudingeri* – Genitalia – Taxonomy.

Coutsis J. G.: 4 Glykonos Street, GR-10675 Athens, Greece. kouts@otenet.gr

## Introduction

The genus *Carcharodus* was erected by Hübner ([1819] 7: 110) and its type-species by designation by the ICZN under its Plenary Powers is *Papilio alceae* Esper, [1780] (Esper 1(Bd. 2): 4, pl. 51, fig. 3). On most occasions, past and present, the following species-group taxa have been placed in *Carcharodus*: *C. alceae* (Esper, [1780]); *C. tripolina* (Verity, 1925); *C. floccifera* (Zeller, 1847); *C. orientalis* Reverdin, 1913; *C. dravira* (Moore, [1875]); *C. baeticus* (Rambur, [1839]); *C. stauderi* Reverdin, 1913 and *C. lavatherae* (Esper, [1783]). This practice has been followed despite the fact that it was well known to the authors that the male genitalia in the group are far from being homogeneous. In fact Higgins (1975), after having illustrated totally dissimilar male genitalia between certain of the skippers belonging in this group, dismissed any attempts at breaking down *Carcharodus* into separate genera by stating that "It does not appear to the author that generic distinction is necessary". No doubt, the criterion for such decisions must be sought in the colour and pattern homogeneity of the wings of these skippers.

Ragusa (1919: 172) was the first author to erect the new genus *Reverdinus* to be applied collectively to *C. alchymillae* Hübner, [1793] (= *C. floccifera*), *C. marrubii* Rambur, [1839] (= *C. baeticus*), *C. stauderi*, and *C. ramses* Reverdin, 1914 (= *C. stauderi*) on morphological grounds; its type-species by subsequent selection by Lindsey (1925: 100) is *Papilio altheae* Hübner, [1800–1803] (= *C. floccifera*). The reason for this generic distinction was based on the fact that the males of the above mentioned taxa exhibited a hair-tuft on FW underside, which was lacking in *C. alceae*. The action was accepted by Verity (1940), who included under this new genus the species-group taxa *marrubii* (= *C. baeticus*) and *alchymillae* (= *C. floccifera*), as well as by Forster & Wohlfahrt (1976), who included under this new genus the species-group taxa *floccifera* and *baeticus*. In both cases this was carried out

on the basis of the presence in the males of these two taxa of the FW underside hair-tuft, as well as because of already known by then extensive differences between the male genitalia of *C. floccifera* and *C. baeticus* on the one hand, and those of *C. alceae* on the other.

Verity (1940: 11, 22) erected yet another genus, that of *Lavatheria*, whose type-species by original designation is *Papilio lavatherae* Esper, [1783], (Esper 1(Bd. 2): 148, pl. 82, fig. 4). The action was based this time on male genitalic character differences between *C. lavatherae* and the rest in the group. Forster & Wohlfahrt (1976) once again obliged by accepting this action which was generally ignored by others.

## A re-description of the male genitalia of species-group taxa presently placed in the genus *Carcharodus*

***C. alceae*** (Fig. 1): Uncus long, slender, mildly hooked downwards at distal tip; dorsum at base with tuft of long, rigid, straight and erect hairs, much as in certain *Muschampia*, such as *M. poggei* (Lederer, 1858), *M. proteus* (Staudinger, 1886) and *M. staudingeri* (Speyer, 1879) (figs. 13a–c respectively). Tegumen short and lacking under it the horizontal, somewhat rigid platform formed by the diaphragm, as is the case in all other members of the group except *C. tripolina*. Valva short, overall triangular in lateral aspect; cuiller short, with roundish distal tip, pointed dorsal projection, and proximal side partly embracing densely spinose distal extremity of stylifer. Ventrums of stylifer in lateral aspect extending basad to curved pointed apex. Aedeagus short, and shaped more like in *M. staudingeri* (fig. 13c) rather than in the *C. floccifera*-subgroup (figs. 3d, 4e, 5d, 6d, 7e) and in *C. lavatherae* (fig. 8d); post-zonal part broad, heavy and asymmetrical to its longitudinal axis; right side mildly bulged and furnished with well developed spines, obvious only in dorsal and ventral aspects; ventrum with a series of small and slender spines placed centrally near

its apex; vesica without cornuti. Vinculum with evenly curved proximal edge. Saccus short.

**C. tripolina** (Fig. 2): as in *C. alceae* but ventrum of stylifer not extending basad to pointed extremity, thus having instead more or less right angle at junction of its proximal and ventral edges. [Note: this taxon, originally described by Verity (1925) as a subspecies of *C. alceae*, was first recognized as a distinct species on the basis of its male genitalia by de Jong (1978a)].

**C. floccifera** (Fig. 3): Uncus as in *C. alceae* but somewhat wider, and dorsal hair tuft absent. Tegumen

long, having under it a horizontal, somewhat rigid platform formed by the diaphragm, upon which rests the anal duct. Valva long, with oblong overall shape in lateral aspect; cuiller wide, smooth, simple in shape, and roughly right-angled in lateral aspect; lower border of stylifer more-or-less semi-circular and fully spinous. Aedeagus long and slender, evenly tapering to distal extremity; vesica with fused oblong cornuti; post-zonal part asymmetrical to longitudinal axis; right side with tiny spines near distal tip. Vinculum with abrupt triangular break on its proximal edge. Saccus long.

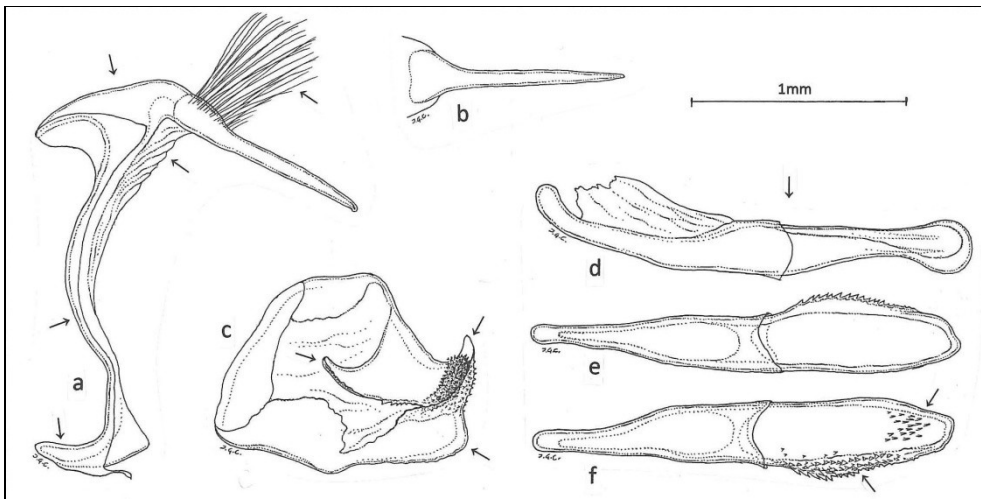


Fig. 1. Genitalia components of male *Carcharodus alceae* (Esper, [1780]), Greece, Ándhros Island, Pláka, 95m, 3.vi.2006. Gen. prep. No. 5618. a. Left lateral aspect of armature, with valvae and aedeagus removed. b. Dorsal aspect of uncus. c. Lateral aspect of inner face of right valva. d – f. Aedeagus. d. Left lateral aspect. e. Dorsal aspect. f. Ventral aspect.

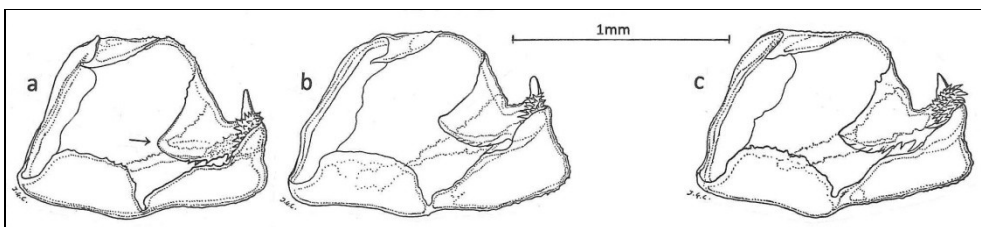


Fig. 2. Lateral aspect of inner face of right valva of male *Carcharodus tripolina* (Verity, 1925). a. Tunisia, Ain Dra-ham, Djebel Bir Kroumirie, 800–1014m, 4.ix.1994. Gen. prep. No. 3002. b. Morocco, Annoeur, Sefrou, Moyen Atlas, 1600m, 11.iv.1983. Gen. prep. No. 3003. c. Spain, Almeria, 0–10km E of El Alquian, 20m, 14 – 16.iv.1987. Gen. prep. No. 3005.

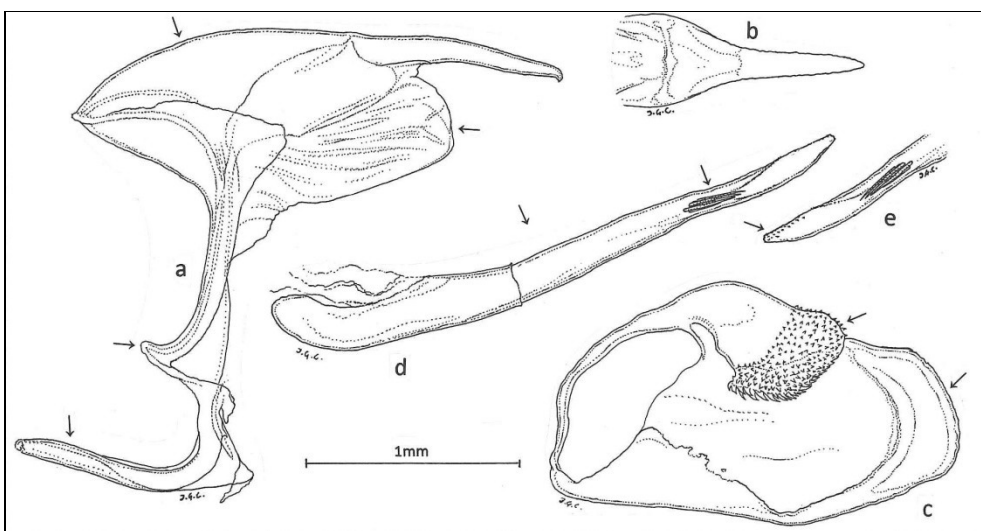


Fig. 3. Genitalia components of male *Reverdinus* (*Reverdinus*) *floccifera* (Zeller, 1847), Greece, Makedhonia, Flórina District, near Pissodhérion, ca. 1400m, 7.viii.1980. Gen. prep. No. 1405. a. Left lateral aspect of armature, with valvae and aedeagus removed. b. Dorsal aspect of uncus. c. Lateral aspect of inner face of right valva. d, e. Aedeagus. d. Left lateral aspect. e. Right lateral aspect of distal end.

**C. orientalis** (Fig. 4): as in *C. floccifera* but, with exception of aedeagus, overall smaller. Valva smaller and more strongly tapering towards distal end; cuiller about half as wide; stylifer smaller, its lower border less rounded, often kidney-shaped, and bearing spines only along its ventro-proximal part, its distal part being smooth.

**C. dravira** (Fig. 5): overall larger than in *C. orientalis*. Cuiller almost as slender as in the latter, but longer;

lower border of stylifer semi-circular and fully spinous, approximately as in *C. floccifera*, but component positioned more upright and placed at a greater distance basad of cuiller and closer to proximal end of valva, thus giving valva entirely different proportions. Aedeagus longer than in all other members of group, and possessing a series of well-developed spines along right side of its post-zonal part. Saccus very long, the longest in the entire group.

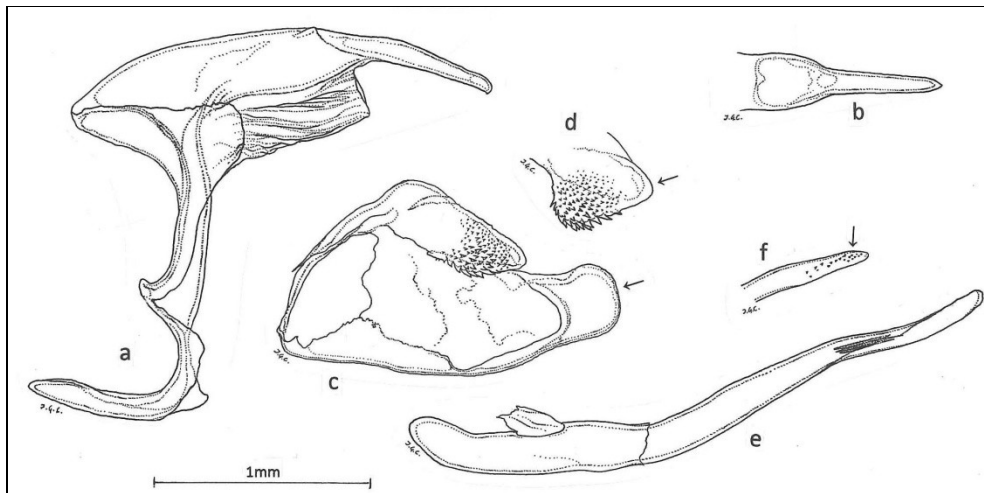


Fig. 4. Genitalia components of male *Reverdinus (Reverdinus) orientalis* Reverdin, 1913, Jordan, Wadi Zarga, 400m, 1km S of Jarash, 13.iv.1997. Gen. prep. No. 3019. a. Left lateral aspect of armature, with valvae and aedeagus removed. b. Dorsal aspect of uncus. c. Lateral aspect of inner face of right valva. d. Flat aspect of stylifer of right valva. e, f. Aedeagus. e. Left lateral aspect. f. dorsal aspect of distal end.

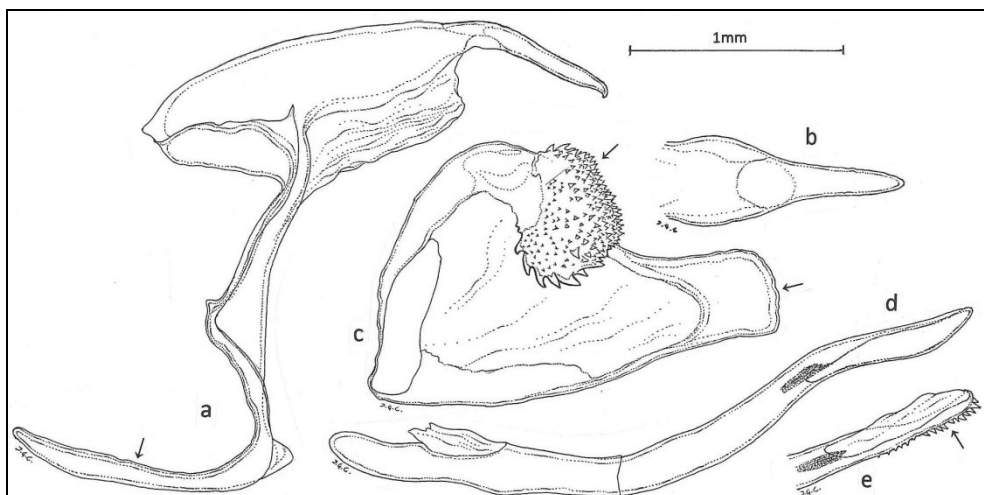


Fig. 5. Genitalia components of male *Reverdinus (Reverdinus) dravira* (Moore, [1875]), Iran, Khoshye alaq, Khush Yailaq, 2000 – 2500m, Gorgan, 28.vi – 2.vii.1971, RMNH. INS. 9000904. Gen. prep. No. 5611. a. Left lateral aspect of armature, with valvae and aedeagus removed. b. Dorsal aspect of uncus. c. Lateral aspect of inner face of right valva. d, e. Aedeagus. d. Left lateral aspect. e. Ventral aspect of distal end.

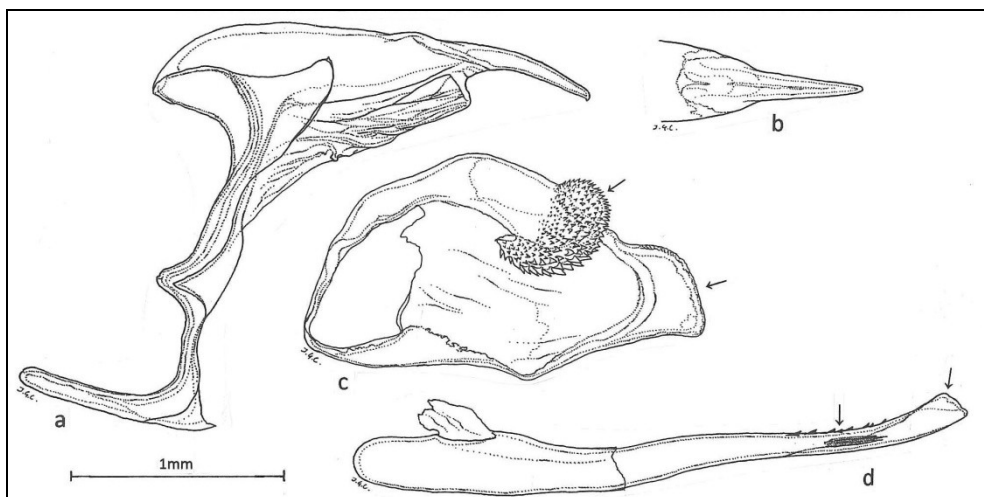


Fig. 6. Genitalia components of male *Reverdinus (Reverdinus) baeticus* (Rambur, [1839]), Spain, Prado Llano, Sierra Nevada, Granada, 2000m, 28.vii.1979. Gen. prep. No. 3010. a. Left lateral aspect of armature, with valvae and aedeagus removed. b. Dorsal aspect of uncus. c. Lateral aspect of inner face of right valva. d. Left lateral aspect of aedeagus.

**C. baeticus** (Fig. 6): overall size approximately as in *C. floccifera*; cuiller somewhat wider than in *C. orientalis*; lower border of stylifer semi-circular and fully spinous, approximately as in *C. floccifera* and *C. dravira*. Aedeagus with small, well-defined dorsal spines along distal half of its post-zonal part, but at a distance from its distal apex; distal apex in lateral aspect often found to possess short, triangular, dorsal extension, probably due to pressure exerted by the eversible vesica.

**C. stauderi** (Fig. 7): as in *C. baeticus* but overall smaller. Stylifer not as large, its lower border less rounded and not fully spinous, having, as does *C. orientalis*, a naked distal extremity. Cornuti in vesica longer than in all other cornuti-bearing taxa in group.

Dorsal spines of aedeagus as in *C. baeticus*, but also invading left lateral part of component.

**C. lavatherae** (Fig. 8): close to all above presented taxa other than *C. alceae* and *C. tripolina*. Overall size about as in *C. floccifera*, but cuiller slender, as in *C. orientalis*, and with toothed, instead of smooth, distal edge; stylifer oblong, fully spinous along its entire length, and almost reaching distal end of cuiller; uncus longer and slightly heavier; horizontally extending diaphragmatic platform, placed under tegumen, considerably deeper; aedeagus shorter, with dorsal bulge near distal extremity, and minute spines mid-ventrally along its distal two thirds; fused cornuti in vesica greater in number.

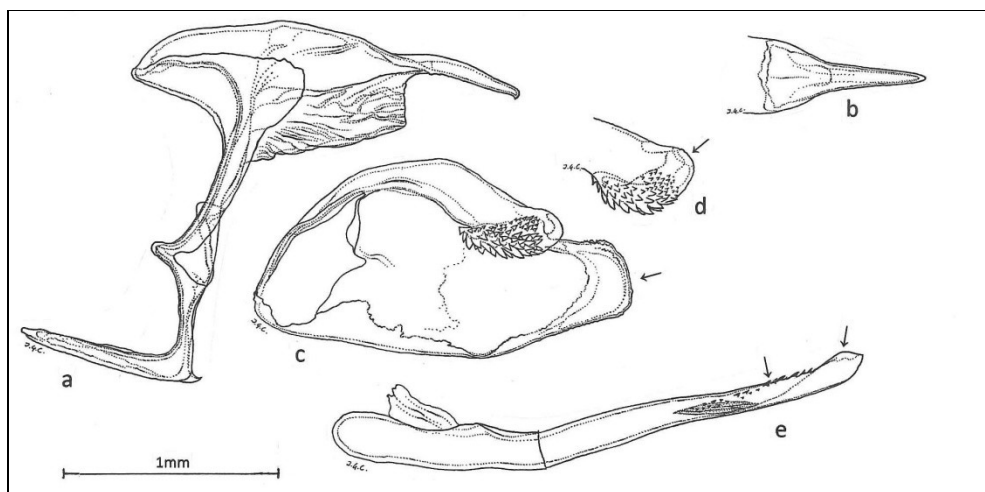


Fig. 7. Genitalia components of male *Reverdinus (Reverdinus) stauderi* Reverdin, 1913, Morocco, Col du Zad, Moyen Atlas, 2200 m, 26.vi.1994. Gen. prep. No. 3012. a. Left lateral aspect of armature, with valvae and aedeagus removed. b. Dorsal aspect of uncus. c. Lateral aspect of inner face of right valva. d. Flat aspect of stylifer. e. Left lateral aspect of aedeagus.

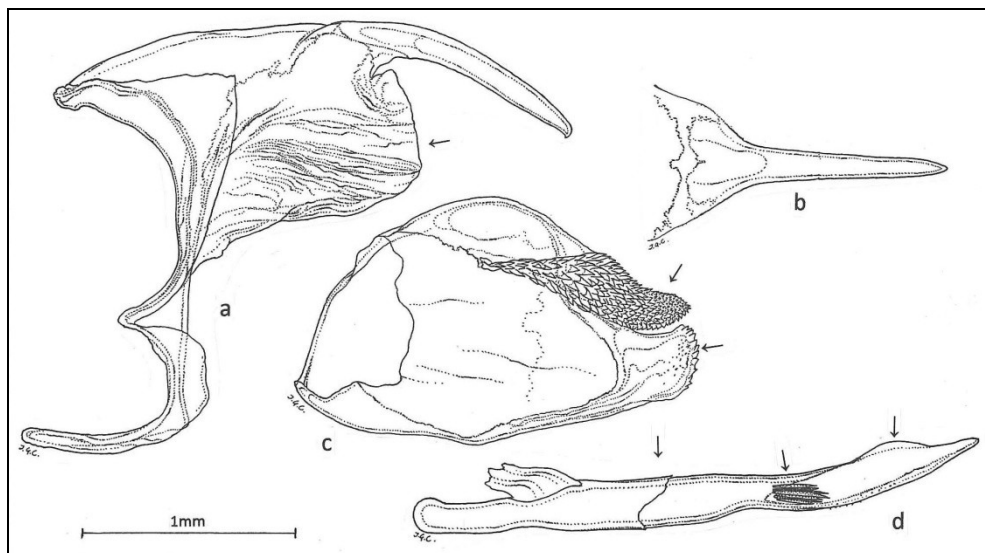


Fig. 8. Genitalia components of male *Reverdinus (Lavatheria) lavatherae* (Esper, [1783]), Morocco, Oukaimeden, Djebel Angour, High Atlas, 2650 m, 1.vii.1994. Col du Zad, Moyen Atlas, 2200m, 26.vi.1994. Gen. prep. No. 3017. a. Left lateral aspect of armature, with valvae and aedeagus removed. b. Dorsal aspect of uncus. c. Lateral aspect of inner face of right valva. d. Left lateral aspect of aedeagus.

### A description and re-description, of components of the female genitalia of species-group taxa presently placed in the genus *Carcharodus*

**C. alceae** (Fig. 9a): central lamella postvaginalis large, heart-shaped, often distally mildly bi-lobed; two lateral ones smaller, shaped like a comma and inverted comma respectively, and placed at a distance from ostium bursae. Papillae anales small and short, with dorso-

lateral rounded protuberance at proximal end, stemming from outer wall of these structures.

**C. tripolina** (Fig. 9b): as in *C. alceae* but central lamella postvaginalis much smaller (about half the size of that of latter), and lateral lamellae postvaginales with differently shaped and smaller distal two thirds.

**C. floccifera** (Fig. 10a): central lamella postvaginalis horizontally oblong, often distally mildly bi-lobed; two lateral ones vertically oblong, often not fully sclerotized throughout and always extending basad to ostium

bursae. Papillae anales large, long, and devoid of any dorso-lateral protuberance [Notes: a. The shape of the lateral lamellae postvaginales in this species, and all the ones that follow, appears variable often because of curling of the component, probably due to desiccation; this means that the readings of these components cannot be accurate enough for making detailed comparisons. b. In the illustrations of the present species and all the ones that follow, the ventral area just basad of ostium bursae, which may or may not incorporate a lamella antevaginalis, has been omitted in order to expose the lateral lamellae postvaginales at full length.]

**C. orientalis** (Fig. 10b): as in *C. floccifera* but overall smaller; central lamella postvaginalis less oblong horizontally. Lateral lamellae postvaginales often with lightly sclerotized area, as in former taxon.

**C. dravira** (Fig. 11a): as in *C. orientalis* but, in the single specimen studied, lateral lamellae postvaginales

are somewhat longer, appear wider and have a slightly sclerotized distal one third.

**C. baeticus** (Fig. 11b): as in *C. orientalis*.

**C. stauderi** (Fig. 12a): as in *C. orientalis* but in seven specimens, all from Sími Island, Greece, and all found to have the lateral lamellae postvaginales with identical lightly sclerotized areas restricted latero-distally along the inner edge of the lamellae; the single specimen from Morocco figured here has the lightly sclerotized area of this component covering about distal one third of its total length.

**C. lavatherae** (Fig. 12b): as in *C. floccifera* but overall larger; central lamella postvaginalis longer but narrower; papillae anales the longest in whole group; apophyses posteriores, attached to papillae anales, massive, quite in contrast to those of the rest in the group.

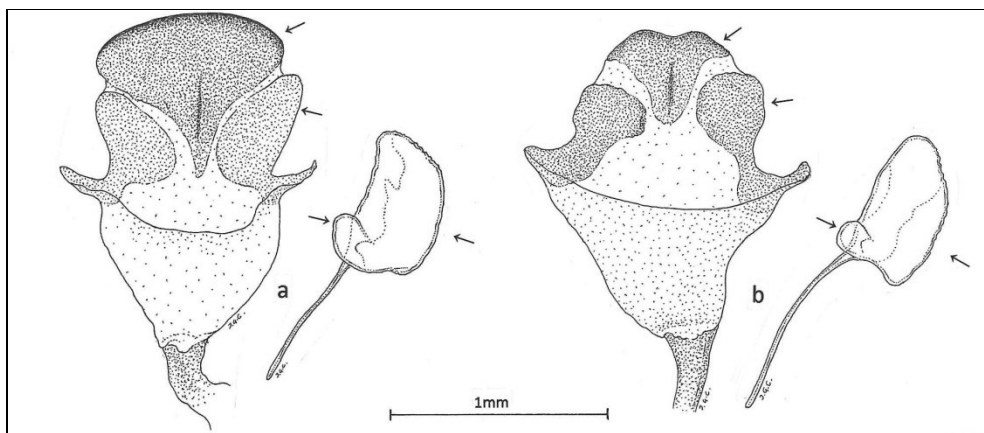


Fig. 9. Genitalia components of female *Carcharodus* species: ventral aspect of lamellae postvaginales (left), together with lateral aspect of exterior face of left papilla analis and its apophysis posterioris (right). a. *C. alceae*, Greece, Ándhros Island, Pláka, 95m, 3.vi.2006. Gen. prep. No. 5543. b. *C. tripolina*, Morocco, Moyen Atlas, Piste au dessus de Aguelmane Sidi Ali, 10.vii.1966, RMNH. INS. 9000906. Gen. prep. No. 5616.

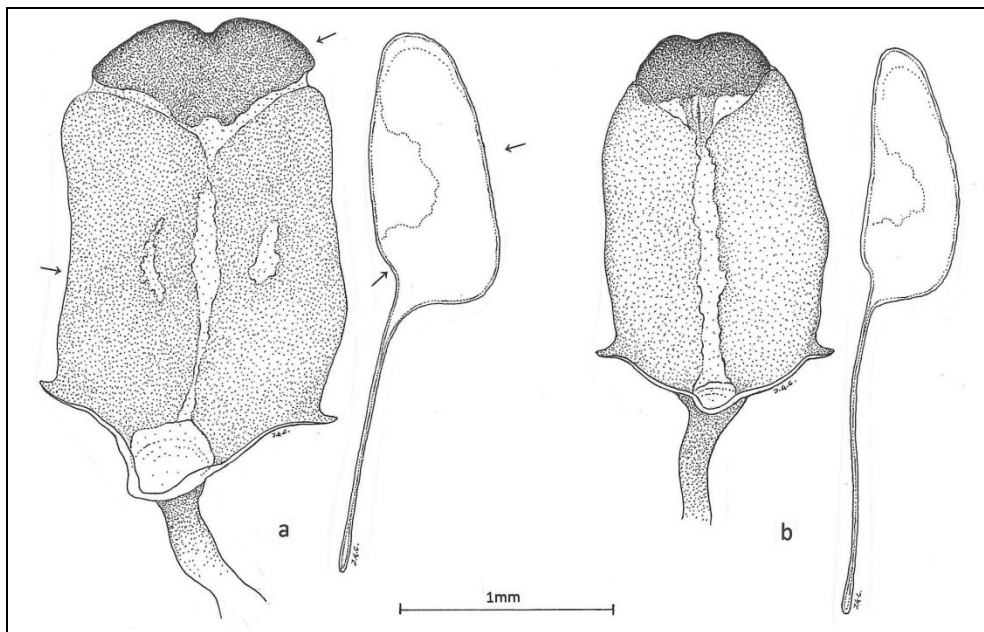


Fig. 10. Genitalia components of female *Reverdinus* species: ventral aspect of lamellae postvaginales (left), together with lateral aspect of exterior face of left papilla analis and its apophysis posterioris (right). a. *R. (R.) floccifera*, Greece, Makedhonía, Rodhópi Mts., 1000–1200m, 10.vii.2000. Gen. prep. No. 5545. b. *R. (R.) orientalis*, Greece, Pelopónnisos, Mt. Trahí, Artemíssio Range, 1200–1250 m, 7.vii.2014. Gen. prep. No. 5544.

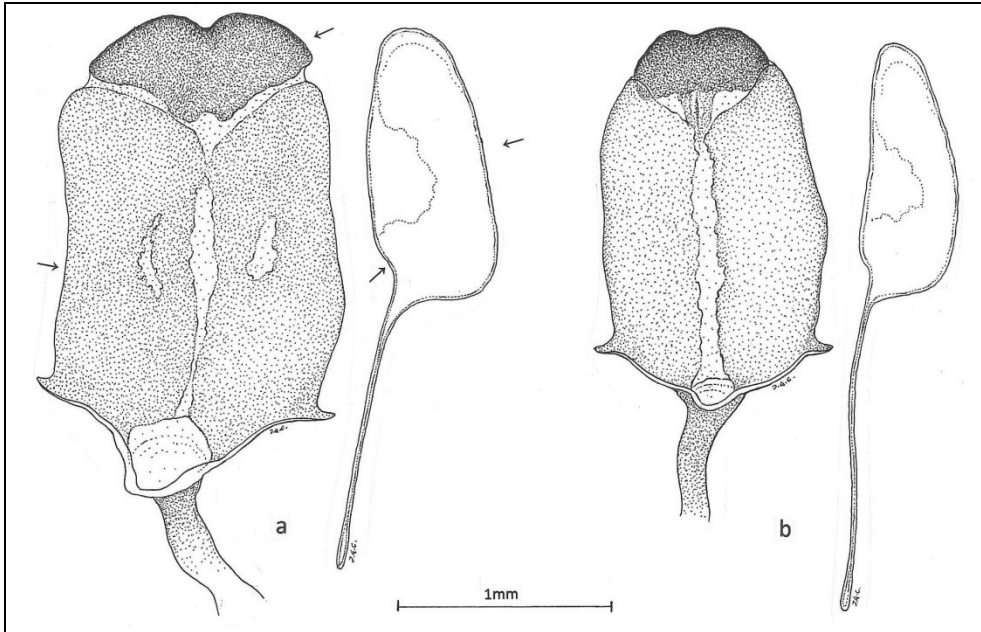


Fig. 11. Genitalia components of female *Reverdinus* species: ventral aspect of lamellae postvaginales (left), together with lateral aspect of exterior face of left papilla analis and its apophysis posterioris (right). a. *R. (R.) dravira*, Iran, Khorasan, Bonjurd, Baba Aman, 1000–1100m, 4.vi.1973, RMNH. INS. 9000905. Gen. prep. No. 5615. b. *R. (R.) baeticus*, Spain, Guenza, Castilla, RMNH. INS. 9000902. Gen. prep. No. 5614.

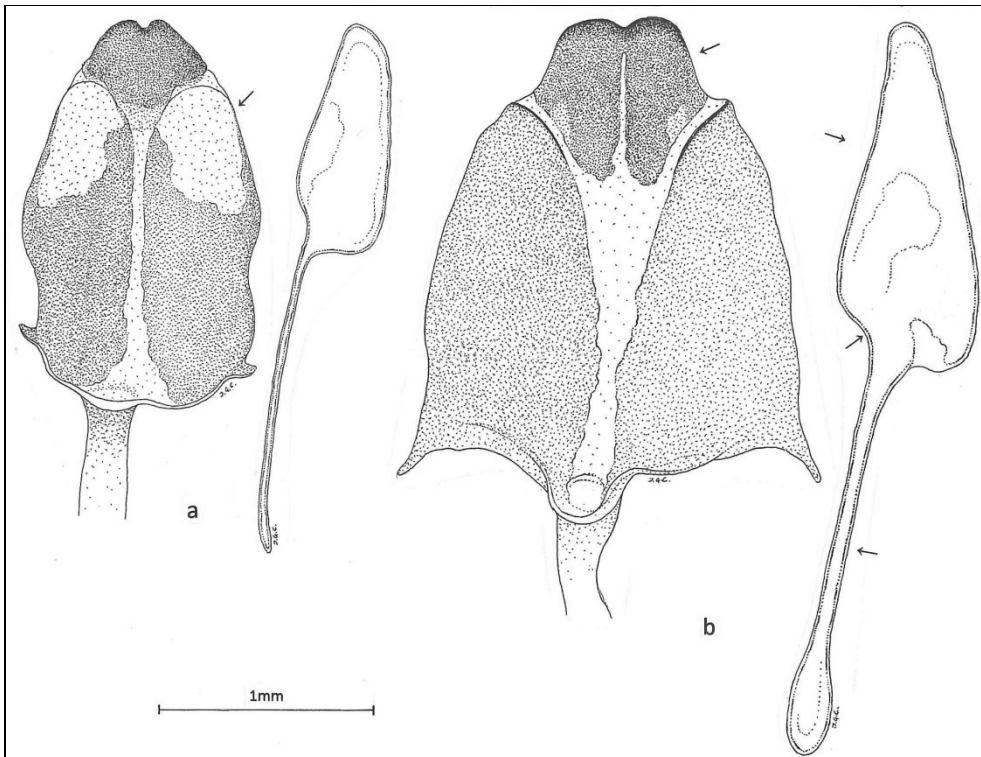


Fig. 12. Genitalia components of female *Reverdinus* species: ventral aspect of lamellae postvaginales (left), together with lateral aspect of exterior face of left papilla analis and its apophysis posterioris (right). a. *R. (R.) stauderi*, Morocco, Col du Zad, Moyen Atlas, 2200m, 28.vii.1975, RMNH. INS. 9000903. Gen. prep. No. 5613. b. *R. (L.) lavatherae*, Greece, Makedhonía, near Nevrokópi, 600–800m, 30.vi.1988. Gen. prep. No. 5612.

### Discussion

Both male and female genitalia of *C. alceae* and *C. tripolina* stand out as being quite unique in the group, differing from those of all other members of the group on just about all counts; in the male there are pronounced differences in the shape and size of the valva, the aedeagus, the vinculum, as well as in the structuring of the diaphragm right under the tegumen, and the length of the saccus; in the female there are extensive differences in the shape and size of the lamellae postvaginales and the papillae anales; furthermore these two taxa share at least one male genitalic character (hair tuft on dorsum of uncus) with members of the separate genus *Muschampia*, and possess an aedeagus that appears closer in shape and

size to that of *M. staudingeri* than it does to any single other member of their own group.

The taxa *C. floccifera*, *C. orientalis*, *C. dravira*, *C. baeticus* and *C. stauderi* have male and female genitalia that are quite uniform and differ from one another only slightly and in detail, clearly suggesting that they represent a single, compact subgroup; all differ considerably, however, from those of *C. alceae* and *C. tripolina*, suggesting a far greater genetic distance from these two taxa. Furthermore all male taxa in the subgroup have a hair-tuft on FW underside, which is absent in both *C. alceae* and *C. tripolina*.

Despite the genitalic uniformity in this subgroup of species there exists no evidence of hybridization between any two of them that are known to be syntopic

and synchronous. This means that clear-cut speciation does not necessarily imply pronounced differences in genitalic characters.

The taxon *C. lavatherae* appears to be an offshoot of the *C. floccifera*-subgroup, possessing on the whole

similar male and female genitalia, but at the same time exhibiting certain character differences that go beyond those extant in the *C. floccifera*-subgroup. Furthermore male *C. lavatherae* lack the FW underside hair-tuft that is present in all members of the *C. floccifera*-subgroup.

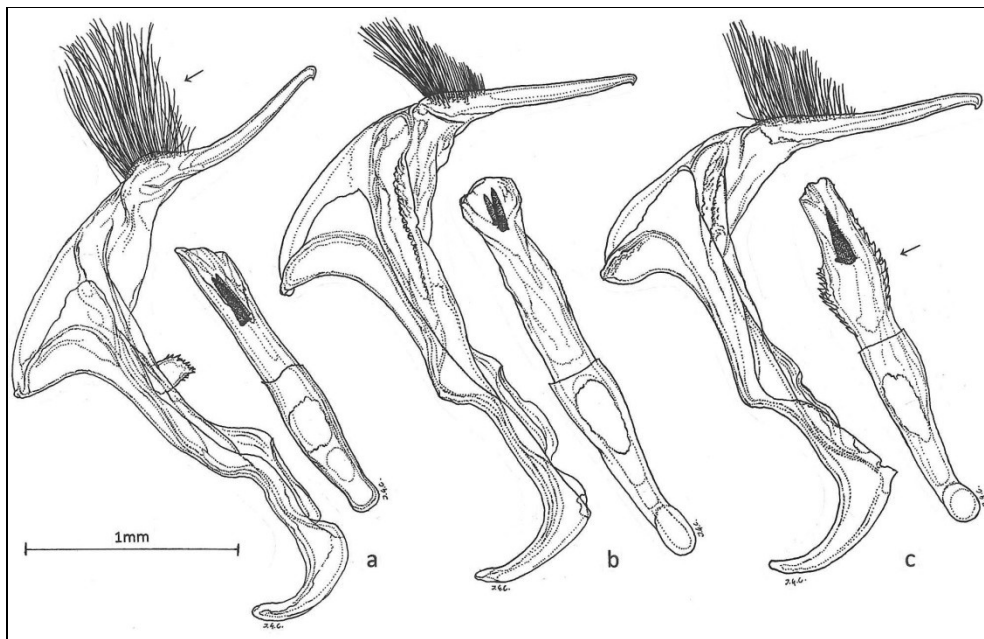


Fig. 13. Genitalia components of male *Muschampia* species: Left lateral aspect of armature with valvae and aedeagus removed (left), together with dorsal aspect of aedeagus (right). a. *Muschampia poggei* (Lederer, 1858), Turkey, Van Province, Kurubaş Geçidi, 29.vi–6.vii.1992. Gen. Prep. No. 2778. b. *Muschampia proteus* (Staudinger, 1886), Tadjikistan, SW Alai Mts., 1700m, Dzhirgatal, 26.vii.1981. Gen. Prep. No. 2782. c. *Muschampia staudingeri* (Speyer, 1879), Turkmenistan, Kara Kala District, Ai-Dere village, 4–13.v.1985. Gen. Prep. No. 2785.

### Conclusions

If one were to accept present day practice of continuing to lump together under the single genus *Carcharodus* the totality of taxa this paper has been presently dealing with, then it would be like turning one's back towards, and virtually ignoring the structural evidence that has been presented, while at the same time it would also mean that the decision for the single genus acceptance for this group of skippers would have to be based solely on commonality of their external characters, such as are those referring to the wings for instance. Wings however may often be dangerously misleading.

If one were to create three subgenera for the group, i.e. those of *Carcharodus*, *Reverdinus* and *Lavatheria*, all under the genus *Carcharodus*, then this would most probably seem appealing to many, but it would not reveal the true essence of the matter, as it would be

implying that all the taxa under consideration are genetically equidistant from each other, which is not the case.

Finally, if one were to split *Carcharodus* into three separate genera, i.e. those of *Carcharodus*, *Reverdinus* and *Lavatheria*, then this would most likely be considered unacceptable to most, and rightfully so, as the species for which the latter two genera would be erected are structurally so close to one another as to preclude separation at generic level.

With all the above in mind it appears logical to the present author that the taxonomical and nomenclatural path best reflecting the conditions that have been exposed and discussed is of generically separating *Reverdinus* from *Carcharodus*, and of considering *Lavatheria* a subgenus of *Reverdinus*.

It is thus proposed that the following taxonomic and nomenclatural arrangements be put to effect:

*Carcharodus alceae* (Esper, [1780])  
*Carcharodus tripolina* (Verity, 1925)

*Reverdinus (Reverdinus) floccifera* (Zeller, 1847)  
*Reverdinus (Reverdinus) orientalis* (Reverdin, 1913)  
*Reverdinus (Reverdinus) dravira* (Moore, 1875)  
*Reverdinus (Reverdinus) baeticus* (Rambur, 1839)  
*Reverdinus (Reverdinus) stauderi* (Reverdin, 1913)

*Reverdinus (Lavatheria) lavatherae* (Esper, [1783])

Species	Uncus	Tegumen	Valva	Cuiller	Stylifer	Aedeagus	Vesica	Vinculum	Saccus	Lameliae postvaginales	Papillae anales
<i>Carcharodus alceae</i>	Less wide than in <i>Reverdinus</i> ; dorsum at base with rigid hair-tuft.	Short, lacking under it horizontal platform formed by diaphragm.	Short, overall triangular in lateral aspect.	Short, with roundish distal tip and pointed dorsal projection.	Ventrum in lateral aspect extending basad to pointed apex.	Short. Post-zonal part broad and heavy; right side mildly bulged with well developed spines.	Cornuti absent.	Proximal edge evenly curved.	Short.	Central one large, heart-shaped; lateral ones comma-shaped and inverted comma-shaped, placed at distance from ostium bursae.	Small and short, with dorso-lateral rounded protuberance at proximal end.
<i>Carcharodus tripolina</i>	As in <i>alceae</i> .	As in <i>alceae</i> .	As in <i>alceae</i> .	As in <i>alceae</i> .	Ventrum in lateral aspect <b>not</b> extending basad to pointed apex.	As in <i>alceae</i> .	As in <i>alceae</i> .	As in <i>alceae</i> .	As in <i>alceae</i> .	As in <i>alceae</i> , but central one much smaller, about 1/2 in size, and lateral ones differently shaped.	As in <i>alceae</i> .
<i>Reverdinus (Reverdinus) floccifera</i>	As in <i>Carcharodus</i> , but somewhat wider, and without dorsal hair-tuft.	Long, with horizontal platform under it formed by diaphragm.	Long, with oblong shape in lateral aspect.	Wide, smooth, simple in shape, roughly right-angled in lateral aspect.	Lower border more- or-less semi-circular and fully spinous.	Long, slender, evenly tapering to distal extremity. Right side of post-zonal part with tiny spines near distal tip.	With fused oblong cornuti.	Proximal edge with abrupt triangular break.	Long.	Central one horizontally oblong. Lateral ones vertically oblong, extending basad to ostium bursae.	Large, long and devoid of any dorso-lateral protuberance.
<i>Reverdinus (Reverdinus) orientalis</i>	As in <i>floccifera</i> , but shorter.	As in <i>floccifera</i> , but shorter.	In lateral aspect as in <i>floccifera</i> , but smaller and more strongly tapering towards distal end.	About half as wide as in <i>floccifera</i> .	Smaller than in <i>floccifera</i> , its lower border less rounded, often kidney-shaped; spines restricted to its ventro-proximal part.	As in <i>floccifera</i> .	As in <i>floccifera</i> .	As in <i>floccifera</i> , but shorter.	As in <i>floccifera</i> , but shorter.	As in <i>floccifera</i> , but smaller.	As in <i>floccifera</i> .
<i>Reverdinus (Reverdinus) dravira</i>	As in <i>floccifera</i> , but shorter.	As in <i>floccifera</i> .	In lateral aspect as in <i>orientalis</i> , but larger, medially considerably wider and more strongly tapering towards distal end.	Almost as slender as in <i>orientalis</i> , but longer.	As in <i>floccifera</i> , but positioned more upright and placed at greater distance basad of culler.	As in <i>floccifera</i> , but longer and with well developed spines along right side of post-zonal part.	As in <i>floccifera</i> .	As in <i>floccifera</i> .	Very long, longest in entire group.	As in <i>orientalis</i> , but lateral ones somewhat longer, wider, with lightly sclerotized distal one third.	As in <i>floccifera</i> .
<i>Reverdinus (Reverdinus) baeticus</i>	As in <i>floccifera</i> , but shorter.	As in <i>floccifera</i> , but shorter.	As in <i>floccifera</i> , but more strongly tapering towards distal end.	Width halfway between that of component in <i>floccifera</i> and <i>orientalis</i> .	Much as in <i>floccifera</i> , but fully spinous lower border even closer to being semi-circular.	As in <i>floccifera</i> , but with small dorsal spines along distal half of post-zonal part.	As in <i>floccifera</i> .	As in <i>floccifera</i> .	As in <i>floccifera</i> , but shorter.	As in <i>floccifera</i> , but smaller.	As in <i>floccifera</i> .
<i>Reverdinus (Reverdinus) stauderi</i>	As in <i>baeticus</i> , but shorter.	As in <i>baeticus</i> , but shorter.	As in <i>baeticus</i> , but smaller.	Narrower than in <i>baeticus</i> , wider than in <i>orientalis</i> .	As in <i>orientalis</i> , but lower border rounder, never kidney-shaped.	As in <i>baeticus</i> , but shorter, and dorsal spines invading left lateral part of component.	As in <i>floccifera</i> , but fused cornuti more numerous.	As in <i>baeticus</i> .	As in <i>baeticus</i> .	As in <i>dravira</i> , but lightly sclerotized area of lateral lamellae usually smaller.	As in <i>baeticus</i> .
<i>Reverdinus (Lavatheria) lavatherae</i>	As in <i>floccifera</i> , but longer.	As in <i>floccifera</i> , but horizontally extending diaphragmatic platform under it considerably deeper.	Overall size and shape as in <i>floccifera</i> .	Narrow as in <i>orientalis</i> , but with toothed distal edge.	Oblong, fully spinous throughout its entire length and almost reaching distal end of culler.	As in <i>floccifera</i> , but shorter, with dorsal bulge near distal extremity, and minute spines mid-ventrally along its distal two thirds.	As in <i>floccifera</i> , but fused cornuti more numerous.	As in <i>floccifera</i> .	As in <i>floccifera</i> , but shorter.	As in <i>floccifera</i> , but central one longer and narrower.	As in <i>floccifera</i> , but heavier and longer, with massive apophyses posteriores

Table 1. Synoptic presentation of genitalia differentiating characters in skippers placed in the genera *Carcharodus* and *Reverdinus*.



## Selected genitalia illustrations in literature

**C. alceae:** Verity 1940, pl. 1, fig. 2 ♂; Evans 1949 pl. 23, fig. 1 ♂; de Jong 1974, p. 3, figs. 1–3 ♂, *alceae* type; Higgins 1975, p. 47, fig. 36(a–c) ♂; de Jong 1978b, p. 118, fig. 1 ♂; Nekrutenko 1985, p. 22, figs. 14(1, 2) ♂, fig. 14(3) ♀; Jakšić 1998, p. 28, figs. 2, 3 ♂; Gorbunov 2001, pl. 3, fig. 4 ♂.

**C. tripolina:** de Jong 1974, p. 3, figs. 4–6 ♂, as *C. alceae*, *tripolinus* type; de Jong 1978a, p. 118, fig. 2 ♂.

**R. (R.) floccifera:** Verity 1940, pl. 1, fig. 4 ♂, as *R. alchymillae*; Evans 1949, pl. 23, fig. 5 ♂; Nekrutenko 1985, p. 22, figs. 16(1) ♂, fig. 16(2) ♀; Higgins 1975, p. 49, fig. 39(a, b) ♂; Tuzov *et al.* 1997, p. 109, fig. 60(1) ♂; Jakšić 1998, p. 28, fig. 6 ♂; Gorbunov 2001, pl. 3, fig. 3 ♂.

**R. (R.) orientalis:** Evans 1949, pl. 23, fig. 5 ♂, as *C. floccifera orientalis*; Higgins 1975, p. 49, fig. 39(c) ♂, as *C. flocciferus orientalis*; Nekrutenko 1985, p. 25, fig. 17 ♂; Tuzov *et al.* 1997, p. 109, fig. 60(2) ♂; Jakšić 1998, p. 28, fig. 5 ♂; Gorbunov 2001, pl. 3, fig. 2 ♂ [Note: the very long saccus and the fully spinous stylifer rather suggest a *R. (R.) dravira*. If the label data are correct – Caucasus, Azish-Tau Range, 6.vi.1996 – then this may be the first record for this species in this area]; Coutsis & Ghavalas 2013, p. 13, fig. 1(B) ♂.

**R. (R.) dravira:** Evans 1949, pl. 23, fig. 5 ♂, as *C. floccifera dravira*; Tuzov *et al.* p. 109, fig. 6(4) ♂; Tshikolovets 1998, pl. XXV, figs. 7, 8 ♂.

**R. (R.) baeticus:** Verity 1940, pl. 1, fig. 3 ♂, as *R. marrubii*; Evans 1949, pl. 23, fig. 3 ♂, as *C. boeticus*; Higgins 1975, p. 49, fig. 38(a) ♂, *C. boeticus boeticus*.

**R. (R.) stauderi:** Evans 1949, 23, fig. 4 ♂; Higgins 1975, p. 49, fig. 38(b, c) ♂, as *C. boeticus stauderi*; de Jong 1978b, p. 208, figs. 1–3, as *C. boeticus stauderi*; Tuzov *et al.* 1997, p. 109, fig. 60(3) ♂; Coutsis & Ghavalas 2013, p. 13, fig. 1(A) ♂.

**R. (L.) lavatherae:** Verity 1940, pl. 1, fig. 5 ♂; Higgins 1975, p. 48, fig. 37(a, b) ♂; Nekrutenko 1985, p. 23, fig. 15(1) ♂, fig. 15(2) ♀; Jakšić 1998, p. 28, fig. 4 ♂; Gorbunov 2001, pl. 3, fig. 1 ♂.

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