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.


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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.

Ragusia (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 genital 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 styliifer. Ventrum of styliifer 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 long, 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.

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**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; 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.

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**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, Keshye 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. Ventral aspect of distal end. 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.

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. flociferata* 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 Simi 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. flociferata* 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.
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.


**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])

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ISSN 0771-5277
<table>
<thead>
<tr>
<th>Species</th>
<th>Uncus</th>
<th>Tegumen</th>
<th>Valva</th>
<th>Cuiller</th>
<th>Styliifer</th>
<th>Aedeagus</th>
<th>Vesica</th>
<th>Vinculum</th>
<th>Saccus</th>
<th>Lamellae postvaginales</th>
<th>Papillae anales</th>
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<tbody>
<tr>
<td>Carcharodus alceae</td>
<td>Less wide than in <em>Carcharodus</em></td>
<td>Short, lacking under horizontal platform formed by diaphragm.</td>
<td>Short, overall triangular in lateral aspect.</td>
<td>Short, with rounded distal tip and pointed dorsal projection.</td>
<td>Ventrum in lateral aspect extending basad to pointed apex.</td>
<td>Short, Post-zonal part broad and heavy; right side mildly bulged with well developed spines.</td>
<td>Cornuă absent.</td>
<td>Proximal edge evenly curved.</td>
<td>Short.</td>
<td>Central one large, heart-shaped, lateral ones comma- and inverted comma-shaped, placed at distance from ostium burse.</td>
<td>Small and short, with dorso-lateral rounded protuberance at proximal end.</td>
</tr>
<tr>
<td>Carcharodus tripolina</td>
<td>As in alceae.</td>
<td>As in alceae.</td>
<td>As in alceae.</td>
<td>As in alceae.</td>
<td>As in alceae.</td>
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<tr>
<td>Reverdinus (Reverdinus) floccifera</td>
<td>As in Carcharodus, but somewhat wider, and without dorsal hair-tuft.</td>
<td>Long, with horizontal platform under it formed by diaphragm.</td>
<td>Long, with oblong shape in lateral aspect.</td>
<td>Lower border more or less semi-circular and fully spinous.</td>
<td>With fused oblong cornuă.</td>
<td>Proximal edge with abrupt triangular break.</td>
<td>Long.</td>
<td>Central one horizontally oblong, lateral ones vertically oblong, extending basad to ostium burse.</td>
<td>Large, long and devoid of any dorso-lateral protuberance.</td>
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<tr>
<td>Reverdinus (Reverdinus) orientalis</td>
<td>As in floccifera, but shorter.</td>
<td>As in floccifera.</td>
<td>In lateral aspect as in floccifera, but smaller and more strongly tapering towards distal end.</td>
<td>Almost as slender as in orientalis, but longer.</td>
<td>As in floccifera.</td>
<td>As in floccifera, but shorter.</td>
<td>As in floccifera, but shorter.</td>
<td>As in floccifera, but smaller.</td>
<td>As in floccifera.</td>
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</tr>
<tr>
<td>Reverdinus (Reverdinus) dravira</td>
<td>As in floccifera, but shorter.</td>
<td>As in floccifera.</td>
<td>In lateral aspect as in orientalis, but larger, mediately considerably wider and more strongly tapering towards distal end.</td>
<td>As in floccifera, but positioner more upright and placed at greater distance basad of cuiller.</td>
<td>As in floccifera, but longer and with well developed spines along right side of post-zonal part.</td>
<td>Very long, longest in entire group.</td>
<td>As in orientalis, but lateral ones somewhat longer, wider, with lighter scleritized distal one third.</td>
<td>As in floccifera.</td>
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<tr>
<td>Reverdinus (Reverdinus) baeticus</td>
<td>As in floccifera, but shorter.</td>
<td>As in floccifera, but shorter.</td>
<td>In lateral aspect as in floccifera, but fully spinous lower border even closer to being semi-circular.</td>
<td>Width halfway between that of component in floccifera and orientalis.</td>
<td>As in floccifera, but with small dorsal spines along distal half of post-zonal part.</td>
<td>As in floccifera, but shorter.</td>
<td>As in floccifera, but smaller.</td>
<td>As in floccifera.</td>
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<tr>
<td>Reverdinus (Reverdinus) staudei</td>
<td>As in baeticus, but shorter.</td>
<td>As in baeticus, but smaller.</td>
<td>Narrower than in baeticus, wider than in orientalis.</td>
<td>As in orientalis, but lower border rounder, never kidney-shaped.</td>
<td>As in baeticus, but shorter, and dorsal spines invading left lateral part of component.</td>
<td>Cornuă longer than in all cornuă-bearing species in group.</td>
<td>As in baeticus.</td>
<td>As in baeticus.</td>
<td>As in baeticus.</td>
<td>As in baeticus.</td>
<td>As in baeticus.</td>
</tr>
<tr>
<td>Reverdinus (Lavotheria) lavotherae</td>
<td>As in floccifera, but longer.</td>
<td>As in floccifera, but horizontally extending diaphragmatic platform under it considerably deeper.</td>
<td>Overall size and shape as in floccifera.</td>
<td>Narrow as in orientalis, but with toothed distal edge.</td>
<td>Oblong, fully spinous throughout entire length and extending distal end of cuiller.</td>
<td>As in floccifera, but fused cornuă more numerous.</td>
<td>As in floccifera, but shorter.</td>
<td>As in floccifera, but stronger.</td>
<td>As in floccifera, but central one longer and narrower.</td>
<td>As in floccifera, but heavier and longer, with massive apophyses posteriores</td>
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**Table 1.** Synoptic presentation of genitalia differentiating characters in skippers placed in the genera *Carcharodus* and *Reverdinus*. 

*Note: The table provides a detailed comparison of various morphological features across different species of 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, tripolina* 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(6); C. *floccifera orientalis*; Nekrutenko 1985, p. 25, fig. 17; Tuzov et al. 1997, p. 109, fig. 60(2); Jakšić 1998, p. 28, fig. 5; Gorbunov 2001, p. 3, fig. 2. [Note: the very long saccus and the fully spiny 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]; Coutts & 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. *marrubi*; Evans 1949, pl. 23, fig. 3; as C. *boeticus*; Higgins 1975, p. 49, fig. 38(3); C. *boeticus baeticus*.

**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); Coutts & 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.

Acknowledgments

All my thanks are due to Dr. Rienk de Jong for having had the kindness to review this paper, as well as for arranging that I get in touch with RMNH (Naturalis), in order to borrow material, and to the Trustees of this Museum as well as to Mrs. Eulàlia Gassó-Miracle, Curator of Lepidoptera, for arranging the loan of specimens from the Museum’s collections, without which the present work would not have been made possible.

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ISSN 0771-5277


