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RESEARCH ARTICLE

A new species of *Sarcophaga* Meigen (*Helicophagella* Enderlein) from southern Spain (Diptera: Sarcophagidae)

Thomas Pape

Abstract

Sarcophaga (*Helicophagella*) *carlestolrai* **sp. n.** is described from southern Spain. Based on a phylogenetic analysis, it is assigned to the *noverca*-group of the subgenus *Helicophagella* Enderlein by the combination of: male sternite 5 with a pad of densely-set short, thick, spine-like bristles on the postero-median margin at the base of each lobe; elongated syntergosternite 7+8; and distiphallus with small vesica, sclerotized and dorsally-directed harpes, and adpressed lateral styles. The species is remarkably different from other members of this subgenus in the greatly expanded and strongly laterally compressed lateral styles and juxta raised into a median hyaline crest. Two longitudinal, largely parallel structures situated ventrally on the distiphallus and proximal to the harpes are interpreted as being the vesica. This unusual shape of vesica is a possible synapomorphy with *S. hirticrus* Pandellé, 1896. The possible monophyly of *Helicophagella* and its division into the mainly copro- or necrophagous *melanura*-group and the snail-feeding *noverca*-group is briefly discussed.

Keywords: Europe, flesh flies, phylogeny, subgeneric classification, taxonomy.

Zusammenfassung

Sarcophaga (*Helicophagella*) *carlestolrai* **sp. n.** wird aus Südspanien beschrieben. Basierend auf einer phylogenetischen Analyse wird die neue Art durch die folgenden Merkmale der *noverca*-Gruppe innerhalb der Untergattung *Helicophagella* Enderlein zugeordnet: Männliches Sternit 5 jeweils mit einem dicht besetzten Polster aus kurzen, dicken, stachelartigen Borsten am postero-medianen Rand an der Basis der Loben; einem länglichen Syntergosternit 7+8; und einem Distiphallus mit kleiner Vesica, sklerotisierten und dorsad gerichteten Harpes und lateral stark kompressten Styli. Die Art unterscheidet sich von den anderen Arten dieser Untergattung durch die stark erweiterten und seitlich komprimierten lateralen Styli und die zu einem medianen hyalinen Kamm ausgezogene Juxta. Zwei longitudinale, weitgehend parallele Strukturen, die sich ventral auf dem Distiphallus und proximal der Harpes befinden, werden als Vesica interpretiert. Diese ungewöhnliche Form der Vesica ist eine mögliche Synapomorphie mit *S. hirticrus* Pandellé, 1896. Die mögliche Monophylie von *Helicophagella* und ihre Unterteilung in die hauptsächlich kopro- oder nekrophag lebende *melanura*-Gruppe und die schneckenfressende *noverca*-Gruppe wird kurz diskutiert.

Introduction

The western European fauna of flesh flies is relatively well known (Léonide & Léonide 1986; Pape 1987; Povolný & Verves 1997; Szpila 2010; Richet et al. 2011; Pape et al. 2015), but new species are continuously discovered in the warmer parts and especially along the Alpine orogenic belt and in the areas bordering the Mediterranean, where significantly higher species richness and endemism are found (e.g., Povolný & Verves 1987; Richet et al. 1995; Whitmore 2011; Whitmore et al. 2018).

The genus *Sarcophaga* Meigen, in the wide circumscription of Pape (1996), Whitmore et al. (2013), and Buenaventura & Pape (2017), which largely equals the tribe Sarcophagini of Verves (1989a, 1989b, 1990), contains some 900 species worldwide. Morphological separation of the species is to a large extent based on the male terminalia, and species complexes appear to exist where the sibling species are differentiated exclusively by the shape of the often highly elaborate distiphallic appendages (e.g., Blackith et al. 2001, 2004; Zhang et al. 2013; El-Ahmady et al. 2018). Morphology may provide substantial arguments for phylogenetic resolution (e.g., Zhang et al. 2013; Wang et al. 2019), but molecular data are needed for more robust phylogenies as a means of reaching a stable classification (e.g., Buenaventura & Pape 2017).

Sarcophaga (s. l.) has been subdivided into numerous genus-group taxa, but considerable disagreement exists on their definitions and circumscriptions (e.g., Shewell 1987; Pape 1996; Verves 1987, 1989a, 1989b; Ye et al. 1998; Lehrer 2013) due to difficulties with homologising distiphallic structures, lack of well-supported phylogenies, and differences in ranking preferences. The present paper describes a new species of *Sarcophaga* from southern

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Spain and discusses its phylogenetic position in the context of the assemblage of 17 species treated by Blackith et al. (1998) as *Sarcophaga* subgenus *Helicophagella* Enderlein, which these authors divided into a *melanura*-group and a *noverca*-group. The isolated description of a species outside of a more comprehensive revision, and based on a single specimen, is here considered justified by the distinctive phallic morphology and its phylogenetic implications. Considering the thorough taxonomic treatment already available for the seven species of this subgenus known to occur in Spain (Peris et al. 1994) and the several other extensive taxonomic treatments of this largely East Palaearctic subgenus (Lehrer 1995; Blackith et al. 1998; Lehrer 2000; Richet et al. 2011), this distinctive species may well be a narrowly distributed endemic. A number of taxonomic papers have dealt with *Helicophagella* (under various circumscriptions) since Blackith et al. (1998), some including the proposal of several species-level synonymies as well as new nominal species proposed in what is here referred to as the *melanura*-group (Lehrer 2000, 2006), but it is beyond the scope of the present paper to unravel species complexes and synonymies that are not directly related to the recognition and classification of the species herewith described as new to science.

Material and methods

The holotype was collected in a flight intercept trap, transferred to 70% ethanol, and later pinned with its terminalia extended. Photography was done using a BK plus Imaging System from Visionary Digital (Palmyra, PA, USA) equipped with a Canon 7D digital camera. Stacks of images from multiple focal planes were combined using Zerene Stacker (Zerene Systems LLC). Figure plates were composed in Photoshop CS6 (Adobe, San Jose, CA, USA).

Label information is given verbatim, using a single forward slash (/) to separate lines on the same label and a double forward slash (//) to separate labels.

Due to the extensive abrasion of the macrosetae of the holotype, chaetotaxy was assessed in part from the presence and size of the setal sockets.

Phylogenetic analyses were conducted in TNT version 1.5 (Goloboff & Catalano 2016). The matrix produced by Blackith et al. (1998) was augmented by adding data for *S. carlestolrai* **sp. n.** (Table 1, see further below). The shape of the vesica within *Sarcophaga* is immensely varied, making homology assessments difficult, and even within *Helicophagella* the vesical configurations certainly are much more complex than the two-state option applied by Blackith et al. (1998). However, condensing the diversity of shapes, sizes and orientations of vesical structures into a few homologous states is a substantial challenge. The following configurations are recognized, here numbered to match the codings in Table 1:

(1) vesica present as a large, bilobed median structure. This is a very vaguely circumscribed state that mainly serves to distinguish the large vesica shared by two of the outgroups, *S. carnaria* (Linnaeus, 1758) and *S. incisilobata* Pandellé, 1896, from the smaller vesica found in *S. haemorrhoa* Meigen, 1826 as well as in the ingroup.
(2) vesica strongly reduced to a median, scale-like structure directed apically. Presented by *S. haemorrhoa*.
(3) vesica forming a small bulge or knob that is directed more or less towards the base of the distiphallus. Present in species of the *noverca*-group except *S.* (*H.*) *hirticrus* Pandellé, 1896 and *S. carlestolrai* **sp. n.**
(4) vesica forming a widely diverging, more or less V-shaped structure. Present in the *melanura*-group.
(5) vesica forming two largely parallel plate-like structures that are separated medially. Present in *S.* (*H.*) *hirticrus* and *S. carlestolrai* **sp. n.** (Fig. 6).

The matrix from Blackith et al. (1998), with *S. carlestolrai* **sp. n.** added to it, was analysed under three different codings (i.e., homology assessments) of the configuration of the vesica: a) vesica of *S. carlestolrai* **sp. n.** coded as unknown/inapplicable, matrix otherwise as in Blackith et al. (1998); b) vesica recoded with state 0 for *S. carnaria* and *S. incisilobata*, state 1 for *S. haemorrhoa*, state 2 for species of the *melanura*-group as well as for *S. carlestolrai* **sp. n.** and *S. hirticrus*, and state 3 for the remaining species of the *noverca*-group; c) vesica recoded with state 0 for *S. carnaria* and *S. incisilobata*, state 1 for *S. haemorrhoa*, state 2 for species of the *melanura*-group, state 3 for species of the *noverca*-group without *S. hirticrus*, and state 4 for *S. carlestolrai* **sp. n.** and *S. hirticrus* (for all codings, see Table 1). Analyses were performed under both equal and implied weights and with characters ordered as in Blackith et al. (1998), i.e., ordering 'tip of harpes, shape' and 'juxtal surface, ornamentation'. The recoded vesical character was treated as unordered in all analyses. Branch support measures were produced by symmetric resampling (SR) calculated from 5,000 replications each, with 10 trees retained and 33% change probability. Nomenclature follows Pape (1996). Morphological terminology follows Merz & Haenni (2000) except for Stuckenberg (1999) for the antenna and Whitmore et al. (2013) for the terminalia.

Taxonomy

Sarcophaga (*Helicophagella*) *carlestolrai* **sp. n.**
(Figs. 1–6)

Type material

Holotype ♂: deposited in the Natural History Museum of Denmark, University of Copenhagen: // SPAIN, Cádiz, / Los Barrios, / 22.vii.2008, A. Verdugo leg. / Intercept flight trap. / Zoological Museum, Copenhagen // Holotype m# / *Sarcophaga* / (*Helicophagella*) / *carlestolrai* Pape, **sp. n.** // zmuc / 00022168 [pinned with text facing down for easy reading] //.

Remarks. The trap was deployed near Valdeinfierno creek (M. Carles-Tolrá, pers. comm.). The holotype is in fair condition, but with several of the strong setae on the dorsum of thorax lost and many setae of the legs and body partly stuck together as a result of the specimen having been dried after removal from the intercept flight trap fluid. The terminalia were dissected and mounted on a piece of cardboard pinned with the specimen.

Diagnosis

A medium-sized species with three postsutural dorsocentral macrosetae, no male mid-femoral ctenidium, median marginal macrosetae on abdominal tergites 4 and 5, male sternite 5 V-shaped, with pad of

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Table 1. Character matrix for selected species of *Sarcophaga* (*Helicophagella*). Adapted from Blackith et al. (1998) by augmenting with *S. carlestolrai* **sp. n.** and formatted for analysis in TNT version 1.5 (Goloboff & Catalano 2016). For descriptions of characters and character states, see Blackith et al. (1998). Coding for vesica in bold; columns a, b and c show alternative codings for character 17 (configuration of vesica) as explained under "Material and methods".

```
xread
27 21                                  a           b c
S_carnaria        001221001021001010101110000 0 0
S_incisilobata    000011000000001010101110000 0 0
S_haemorrhoa      010101101020111010001110001 1 1
S_altitudinis     000201000121010101111113001? 3 3
S_dreyfusi        100221010011011101011103311? 3 3
S_gorodkovi       000220000011010101111113000? 3 3
S_inopinata       000111001011010101111200?? 3 3
S_maculata        100221010011011101111331?? 3 3
S_macrura         100221000010101010111103001? 3 3
S_melanura        100211000021010101111103001? 3 3
S_ora             000221010011010101111103311? 3 3
S_pachyura        000221000011011101111200?? 3 3
S_agnata          010202001110011010020110001? 2 2
S_crassimargo     100102001020011010020112000 2 2
S_hirticrus       020112000000011011120100001 3 4
S_novella         000202000120011010020110??? 2 2
S_noverca         000211000110011012020110001 2 2
S_novercoides     000211000020011010020111001? 2 2
S_okaliana        000211000020011010020211??? 2 2
S_rosellei        000201001010011010020110000 2 2
S_carlestolrai    ?102220000000110?00202100?? 3 4
;
```

densely set short and thick spine-like bristles at the base of each lobe. Male terminalia with syntergosternite 7+8 elongate, epandrium longer than high, phallus with harpes turned laterally and slightly dorsally (= posteriorly), juxta hyaline and raised into a median crest, with dorsal margin sclerotized and curved backwards into a sharply pointed tip, lateral styles laterally compressed and united to form a single wide aperture.

Description

Male (holotype). Length = 15 mm from tip of lunule to posterior surface of epandrium (measured before extension of male terminalia). *Colour.* Head black, with dense golden-grey microtrichosity on parafacial, gena and fronto-orbital plate, changing with the incidence of light. Frontal vitta black. Antenna: pedicel black with brown apex; postpedicel black with grey microtrichosity. Prementum black, palpus black with brown tip. Ground colour of thorax black, grey-microtrichose with three longitudinal dark vittae, the middle one bordered by two narrow vittae anterior to suture. Legs black. Tegula black; basicosta light yellow. Abdomen black, densely grey-microtrichose laterally and on entire tergite 5, microtrichosity forming a chequered pattern changing with the incidence of light. Syntergosternite 7+8 blackish brown, with a circular spot of grey microtrichosity posteriorly; epandrium shiny black. Cercus black; surstylus dark brown; gonites dark brown; phallus with sclerotized parts brown to blackish. *Head*. Arista gradually tapering, strongly plumose. Postpedicel almost 3x as long as pedicel. Frons at narrowest point 0.2x head width in anterior view. Frontal vitta about half as wide as frons at narrowest point, widening gradually to double the width towards antennal insertion (dorsal view). Median vertical seta developed; lateral vertical seta weak (small socket). One pair of reclinate fronto-orbital setae. Fronto-orbital plate with several scattered short setulae. Parafacial with scattered short setulae in a row between facial ridge and eye margin, with the lower

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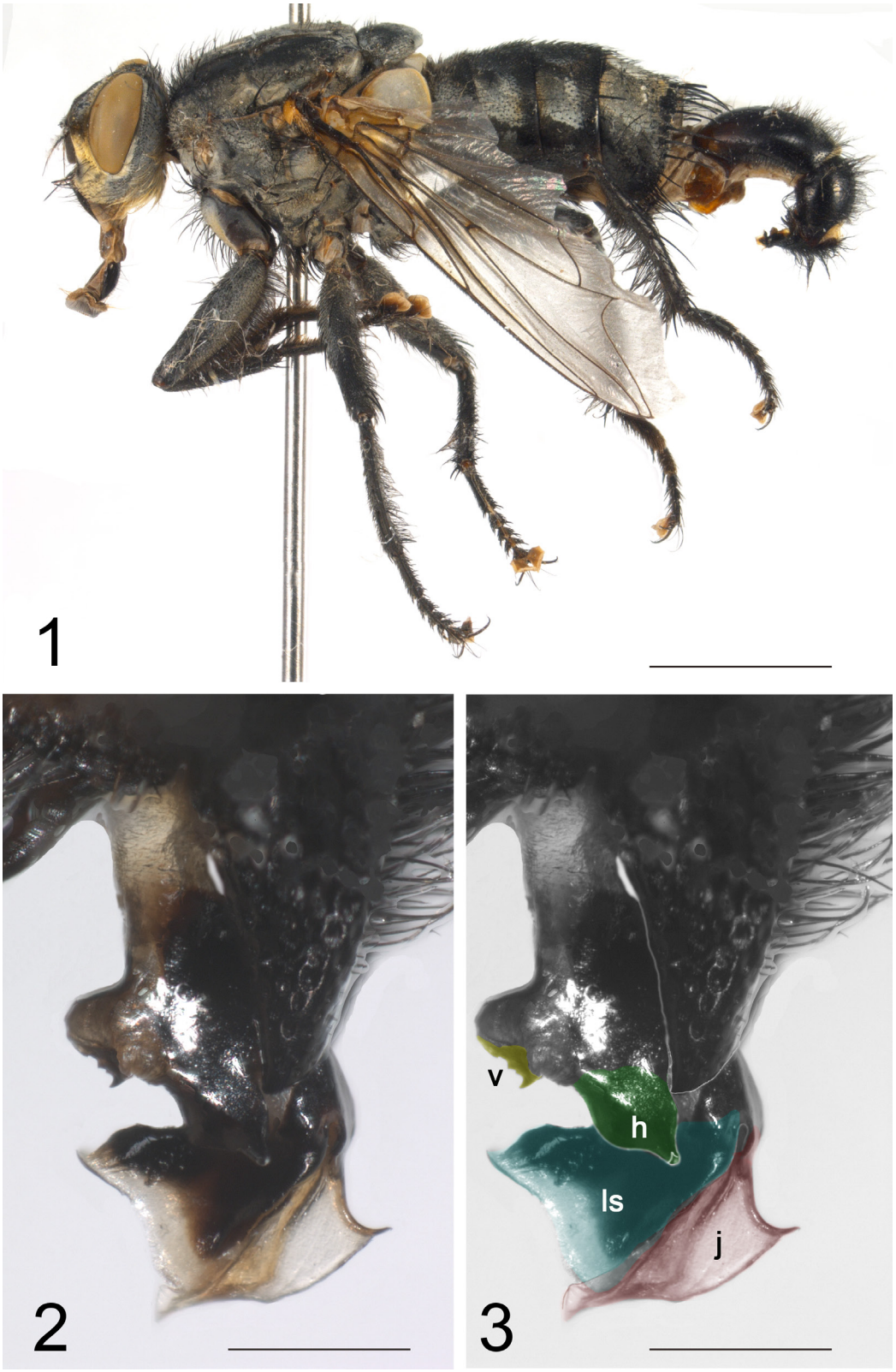

Figs. 1–3. *Sarcophaga* (*Helicophagella*) *carlestolrai* **sp. n.** Holotype ♂ (Spain: Cádiz). **1**. Habitus, left lateral view. **2**. Distiphallus (and tip of left cercal prong), left lateral view. **3**. Distiphallus with appendages colour-coded: yellow = vesica; green = harpes; blue = lateral style; red = juxta. Abbreviations: h = harpes; j = juxta; ls = lateral style; v = vesica. Scale bars: 1 = 3.75 mm; 2, 3 = 0.25 mm.

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Fig. 4–6. *Sarcophaga* (*Helicophagella*) *carlestolrai* **sp. n.** Details of distiphallus. **4**. Dorsal view. **5**. Ventral view. **6**. Lateral view, slightly skewed to show configuration of vesica. Scale bars: 0.5 mm.

5–6 setae stronger and arranged in an irregular patch a little above the lower eye margin. Parafacial at narrowest point 0.46x as wide as minimum eye width in strict lateral view. Lower facial margin slightly visible in lateral view below vibrissa. Facial ridge, above vibrissa, with some decumbent setulae reaching about a quarter of the distance between vibrissal angle and base of postpedicel. Gena in profile 0.6x vertical eye height (measured in same vertical plane as height of head); setulae on gena black except for those next to the genal suture; postgenal setulae pale. Two rows of black occipital setulae behind postocular setae, remaining occipital setulae pale whitish. Prementum 2.5x as long as wide. *Thorax*. Postpronotum with 2 long, strong outer setae and 1 shorter and finer inner seta arranged in an obtuse triangle. Scutum with 0+0 acrostichal setae, 2 (short and fine) + 3 dorsocentral setae, 1 posthumeral seta, 1 presutural seta, 2 primary + 2 subprimary notopleural setae, 2 intra-alar setae and 3 supra-alar setae. Postalar callus with 2 setae. Postalar wall setulose. Prosternum setulose on posterior third. Propleuron bare. Katepisternum with 3 setae arranged almost in a line, the middle one shorter and finer, closer to and a little below the anterior one. Katepimeron bare. Scutellum with 1 pair of basal setae, 1 pair of subapical setae, 1 pair of small apical setae; no discal setae. *Legs*. Mid femur without a ctenidium. Hind trochanter with median surface covered with unmodified setae. *Wing*. Costal spine not developed. Vein R_1 bare dorsally. Short setulae on dorsal surface of vein R_{4+5} extending approximately halfway to crossvein r-m. Cell r_{4+5} open at wing margin. *Abdomen*. Syntergite 1+2 and tergite 3 without median marginal setae. Tergite 4 with a pair of median marginal setae and tergite 5 with

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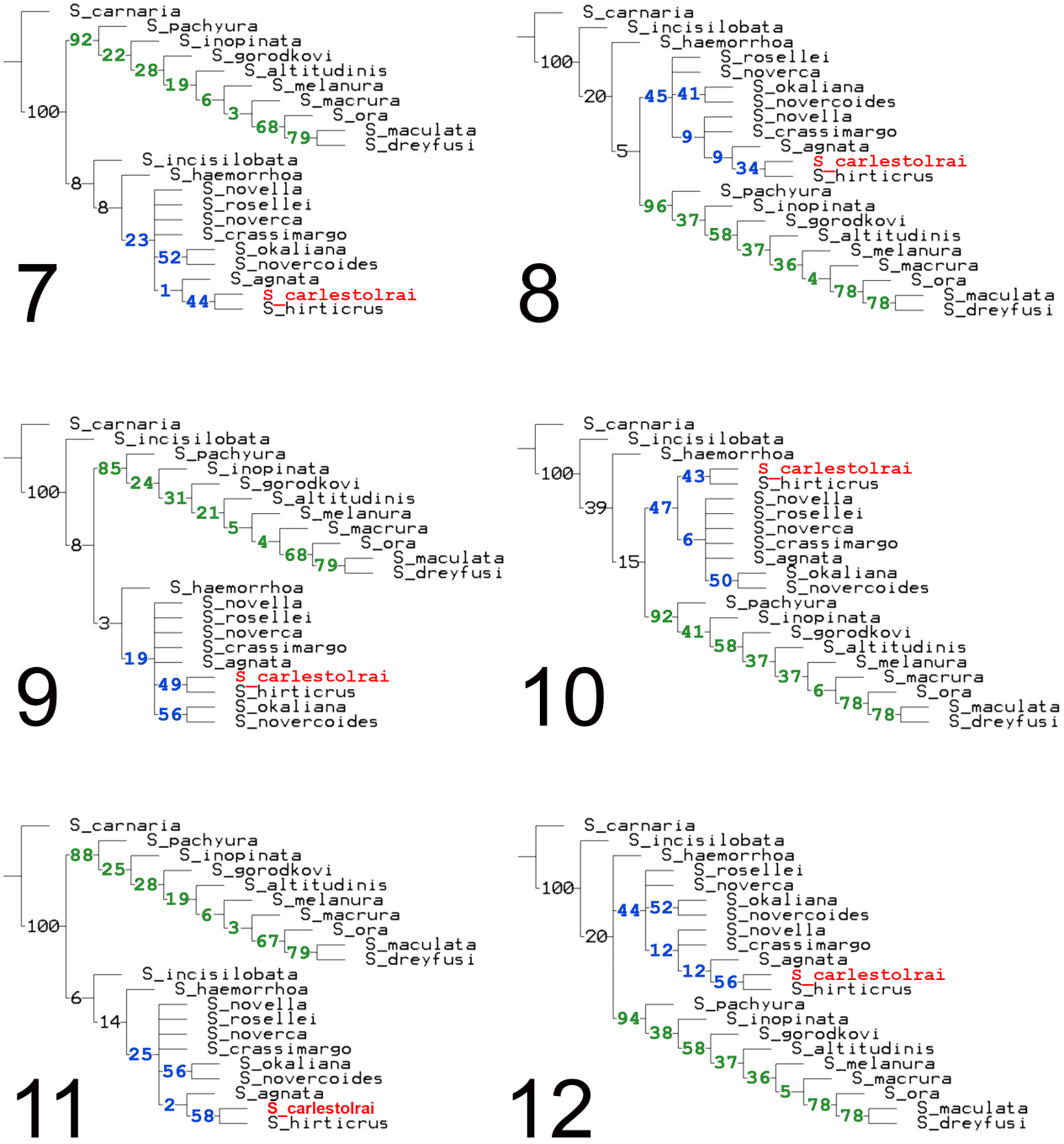

Figs. 7–12. Cladograms obtained from analysis of data in Table 1, with all characters except 17, 18, 24 ordered, under various codings of the vesica and with equal (Figs. 6, 8, 10) or implied (Figs. 7, 9, 11) weighting. **7, 8**. Vesica of *S. carlestolrai* **sp. n.** coded as unknown/inapplicable (Table 1, column a). **9, 10**. Vesica of *S. carlestolrai* **sp. n.** and *S. hirticrus* coded as species of the *melanura*-group (Table 1, column b). **11, 12**. Vesica of *S. carlestolrai* **sp. n.** and *S. hirticrus* coded with an identical separate state (Table 1, column c). Numbers on branches are symmetric resampling percentiles (green for the *melanura*-group, blue for the *noverca*-group).

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a complete row of marginal setae. Sternite 5 with median ridge raised and strongly indented, V-shaped; base of each lobe with a pad of densely-set, short, thick spine-like bristles. *Terminalia*. Syntergosternite 7+8 elongate, 2.5x as long as high, without marginal setae. Epandrium about twice as long as high. Cercus straight, rather short and thick. Pregonite and postgonite slender, curved at tip, of about the same length; pregonite rounded in apico-dorsal view. Phallus without a swelling of the ventral membrane connecting basi- and distiphallus; vesica small, bilobed, with lobes clearly separated, each lobe with a small distal tooth-like process; harpes large, strongly sclerotized and turned laterally and slightly dorsally, gradually tapering; juxta hyaline, following dorsal margin of lateral styles and raised into a median crest with dorsal margin sclerotized and curved backwards into a sharply pointed tip; lateral style laterally compressed, greatly expanded distally, the two lateral styles closely adpressed or united to form a single, almost slit-like aperture with membranous rim.

Female. Unknown.

Distribution

Palaearctic—Spain (Cádiz Province).

Biology

Unknown.

Etymology

The species epithet is given in recognition of Miguel Carles-Tolrá, for his substantial contributions to the exploration of Diptera from the Iberian Peninsula and Balearic Islands.

Discussion

Blackith et al. (1998) provided a morphology-based phylogenetic analysis in which the taxon *Helicophagella* emerged as monophyletic based on only one character state change: harpes changed from ventrally directed to laterally directed. In their favoured cladogram, the *noverca*-group was supported by harpes directed dorsally and a complete reduction of the median stylus. The *melanura*-group was supported by a non-microtrichose ("apollinose") syntergosternite 7+8, pregonite narrowly pointed in apico-dorsal view, vesical lobes flattened and directed ventro-laterally, and juxtal hinge in an apico-dorsal position.

Sarcophaga carlestolrai **sp. n.** matches species of the *noverca*-group in the shape and direction of the harpes. However, the absence in *S. carlestolrai* **sp. n.** of the rather homogeneous, strongly sclerotized median structure situated proximo-ventrally on the distiphallus of all members of the *noverca*-group except *S. hirticrus* is noteworthy. The homology of this structure is debated, i.e., whether it is part of the vesica (Blackith et al. 1998, present paper) or not (Whitmore et al. 2013), but irrespective of the homology, *S. carlestolrai* **sp. n.** does not possess this structure, and what is here interpreted as a vesica is similar to the medially split and flattened vesica of *S. hirticrus*. Re-analysing the morphological matrix produced by Blackith et al. (1998) with the inclusion of *S. carlestolrai* **sp. n.** and with various codings of the vesica as explained above under 'Material and methods' gave the phylogenetic topologies shown in Figs. 7–12. It is noteworthy that the taxon *Helicophagella* as circumscribed by Blackith et al. (1998) is corroborated only under implied weighting and with very low support (Figs. 8, 10). The *melanura*-group is strongly supported in all analyses (SR ≥ 88). The *noverca*-group with *S. carlestolrai* **sp. n.** included received low to moderate support (SR: 19–47). *Sarcophaga hirticrus* and *S. carlestolrai* **sp. n.** emerged as sister species in all analyses, although with only moderate support (SR: 34–58).

While the assignment of *S. carlestolrai* **sp. n.** to *Helicophagella* appears well supported on the morphological evidence alone, molecular data will most likely be needed to settle whether *Helicophagella* in the present circumscription is supported. No molecular data are so far available for *S. carlestolrai* **sp. n.**, and only sparse data are available for other species of *Helicophagella* as well as for species of the subgenera generally considered phylogenetically close. In the molecular study of Buenaventura et al. (2017), *S. melanura* Meigen, 1826 was pruned as a rogue taxon due to data insufficiency, and the eight other species of *Helicophagella* included did not constitute a monophylum but emerged in three separate clades. In Buenaventura & Pape (2017), both *S. melanura* and *S. hirticrus* emerged as isolated from the other included species of *Helicophagella*, whereas Jafari et al. (2019) and Ren et al. (2020) had *S. melanura* as the only representative of the subgenus *Helicophagella*.

The possible sister-group relationship between *S. hirticrus* and *S. carlestolrai* **sp. n.** is interesting, because several widely different hypotheses have been proposed regarding the phylogenetic position of *S. hirticrus*. Verves (1987), when proposing the taxon *Parabellieria* (equivalent to the present *melanura*-group), included *S. hirticrus* but later transferred this species to the taxon *Heteronychia* Brauer & Bergenstamm (Verves 1993). Lehrer (1995) proposed the monotypic genus *Karovia* to accommodate *S. hirticrus*, but this is not supported by the present analysis as it would require most other species in the *noverca*-group to be similarly accommodated in monotypic subgenera.

In light of the current analyses and the biological differences between the mainly copro- or necrophagous species of the *melanura*-group and those of the mainly snail-feeding *noverca*-group (Povolný & Verves 1997), a classification of these two groups within separate sub-

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genera may be both appropriate and convenient. The relevant subgeneric names would be *Parabellieria* Verves, 1987, with type species *Sarcophaga melanura* Meigen, 1826 by original designation, and *Helicophagella* Enderlein, 1928, with type species *Sarcophaga noverca* Rondani, 1861 by original designation. However, as mentioned by Pape & Whitmore (2022), a proper decision should be based on further analyses of subgeneric relationships within *Sarcophaga* (s. l.), preferably based on extensive molecular data.

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