



## Phylogeny and re-definition of the genus *Melanophora* (Diptera: Rhinophoridae), with description of a new species from Sardinia\*

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### Abstract

A cladistic analysis of the genus *Melanophora* Meigen, 1803 (type-species: *Musca grossificationis* Linnaeus, 1758 [= *Musca roralis* Linnaeus, 1758]) is presented and the generic delimitation is critically redefined. The nominal genus-group taxon *Bequaertiana* Curran, 1929 (type-species: *Bequaertiana argyriiventris* Curran, 1929) is synonymised with *Melanophora* Meigen **syn. nov.** The following new combinations are proposed: *Melanophora argyriiventris* (Curran, 1929) **comb. nov.** and *Melanophora basilewskyi* (Peris, 1957) **comb. nov.** *Melanophora chia* **sp. nov.** from SW Sardinia is described, illustrated and compared with the other known species of the genus. The male of *Melanophora asetosa* Kugler, 1978 is described for the first time. *Melanophora basilewskyi* (Peris, 1957) is recorded from Kenya for the first time.

**Key words:** *Melanophora*, *Bequaertiana*, phylogeny, systematics, Sardinia, new species, new combinations

### Introduction

The genus *Melanophora* was erected by Meigen (1803) to include the single species *Musca grossificationis* Linnaeus, 1758 [= *Musca roralis* Linnaeus, 1758]. The genus has largely been maintained as monotypic, defined by some very characteristic features like the long-petiolate wing cell  $r_{4+5}$  and a marked sexual dimorphism in the shape of the antennal arista (bottlebrush-like in the male, usually bare in the female) as well as in the wing pattern (females with a whitish spot at the tip, males without). This sexual dimorphism is so pronounced that it led Robineau-Desvoidy (1830) to accommodate females of *Melanophora roralis* in the genus *Melanophora*, and males of the same species in his new genus *Illigeria*.

The nominal species *Melanophora helicivora* Goureaux, 1843 was bred from a snail and therefore could not reasonably be a member of the exclusively woodlouse-parasitising Rhinophoridae. Only after Séguy (1941: 386) had placed it in the Tachinidae and Pape (1986: 17) tentatively suggested an assignment to the Calliphoridae was its true identity discovered: Pape (1996: 35) synonymised it with *Nyctia halterata* (Panzer, 1798) of the Sarcophagidae.

Kugler (1978) described *Melanophora asetosa* from Israel, which by sharing a number of the distinctive features of *M. roralis* at least superficially would seem to fit nicely as a sister species to the latter. However, as mentioned by Pape (1986) the sparse morphological evidence available actually pointed to *M. asetosa* being more closely related to the Afrotropical genus *Bequaertiana* Curran, 1929 than to *M. roralis*.

The surprising discovery of a hitherto unknown species morphologically very similar to *Melanophora roralis* was an incentive to combine a description of the new species with an analysis of its phylogenetic relationship, in order to support our decision of genus-level assignment and classification.

## Material and methods

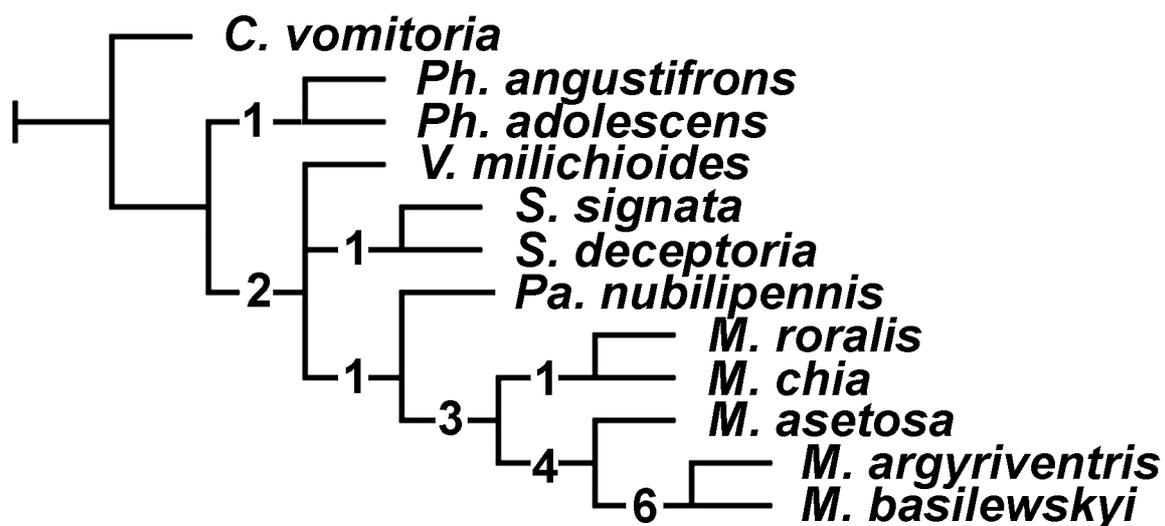
**Specimens:** Uncoated, pinned specimens were examined with a Hitachi TM1000 scanning electron microscope (SEM). Photomicrographs are composites of images captured using a Nikon DS-L1 digital camera mounted on a Leica MZ 12.5 stereoscopic microscope. Composite images were created using Auto-Montage Pro software. Material examined is preserved in the following collections (acronyms used in the text): MZUR: Museum of Zoology, Università degli Studi di Roma “La Sapienza”, Rome, Italy; TAU: Department of Zoology, Tel Aviv University, Tel Aviv, Israel; ZMUC: Natural History Museum of Denmark, Zoological Museum, University of Copenhagen, Denmark.

**Terminology:** Morphological terminology generally follows Merz and Haenni (2000), except for the antenna, for which we are following Stuckenberg (1999). Measurements and ratios of the head follow Tschorsnig and Richter (1998).

**Phylogenetic analysis:** All species currently placed in *Melanophora* and *Bequaertiana*, plus selected species from the genera *Paykullia* Robineau-Desvoidy, *Phyto* Robineau-Desvoidy, *Stevenia* Robineau-Desvoidy and *Ventrops* Crosskey were included in the phylogenetic analysis. For proper rooting of the cladogram, we included *Calliphora vomitoria* (Linnaeus). A matrix containing 34 morphological characters was produced (Appendix 1) and analysed in TNT version 1.1 (Goloboff *et al.* 2003). Multistate characters were treated as unordered and zero-length branches collapsed. Analysis was run as implicit enumeration with equal weighting as well as with implied weights (concavity factor of 1 and higher). Bremer support values were calculated in TNT by saving all suboptimal trees up to 10 steps longer than the shortest as obtained from an implicit enumeration. No resampling analysis was carried out, as the interpretation of the resulting percentiles when performed on a small and highly selective morphological dataset is spurious.

## Results

A total of 34 characters containing 76 character states were coded for 11 species of Rhinophoridae and one species of Calliphoridae (Appendix 1). The three equally most parsimonious phylogenetic trees implied by the data are visualised by the strict consensus tree given in Fig. 1.



**FIGURE 1.** Strict consensus of 3 equally parsimonious trees found by TNT (total length = 48 steps). Numbers on branches denote Bremer support values.

## Systematics

### Genus *Melanophora* Meigen

*Melanophora* Meigen, 1803: 279. Type-species: *Musca grossificationis* Linnaeus, 1758 [= *Musca roralis* Linnaeus, 1758], by monotypy.

*Illigeria* Robineau-Desvoidy, 1830: 273. Type-species: *Illigeria atra* Robineau-Desvoidy, 1830 [= *Musca roralis* Linnaeus, 1758], by subsequent designation (Townsend, 1916: 7).

*Bequaertiana* Curran, 1929: 14. Type-species: *Bequaertiana argyrivertris* Curran, 1929, by original designation.  
**Syn. nov.**

**Recognition.** Facial profile receding (Figs 2, 4) (when postcranial surface is oriented vertically, vibrissal angle is about in line with anterior margin of eye); both sexes with a row of 3–7 proclinate orbital setae (Figs 2, 4); dorsalmost pairs of frontal setae not crossed medially; male arista with bottlebrush-like trichia (Figs 3, 18); scutellum with one or two pairs of marginal setae; wing cell  $r_{4+5}$  long petiolate or M vein ending in the membrane approximately where bend of M should be (Figs 9–10, 14, 20).

**Distribution.** West Palaearctic, Cape Verde Islands, tropical Africa; (introduced in the New World) (*cf.* Herting 1961; Guimarães 1971; Crosskey 1977; Crosskey 1980; Wood 1987; Peris & González-Mora 2007).

### Key to species of *Melanophora*

- 1 M vein complete, wing cell  $r_{4+5}$  closed and long petiolate (Figs 9–10). Crossed apical scutellar setae present and well developed (Fig. 8). Mouthparts well developed (Figs 2, 4). Female: wing membrane mainly brownish with whitish posterior subapical spot (Fig. 10) ..... 2
- M incomplete and not reaching wing margin, ending about where bend of M should be (Figs 14, 20). Scutellum without crossed apical setae. Mouthparts strongly reduced, vestigial (Fig. 13). Female wing pattern not as above ... 3
- 2 Petiole of  $R_{4+5}$  very long, 2.1–2.5 times as long as postangular section of M;  $Cs_6$  at least as long as  $Cs_4$  (distinctly longer in female); anterodistal edge of wing with a concavity at the intersection of 4<sup>th</sup> and 6<sup>th</sup> costal sections, very pronounced in female, just visible in male (Figs 9, 10). Female head and thorax mainly yellow in ground colour. Male cerci, in posterior view, very narrow; basally not enlarged (Fig. 11) ..... *M. chia* sp. nov.
- Petiole of  $R_{4+5}$  0.9–1.6 times as long as postangular section of M.  $Cs_6$  distinctly shorter than  $Cs_4$ . Wing without concavity. Female head and thorax black or dark brown. Male cerci basally enlarged (Fig. 12) ... *M. roralis* (Linnaeus)
- 3 Intra-alar setae present. Thorax and abdomen (Fig. 16) practically without microtomentum.  $R_1$  bare. Mid tibia with 1 anterodorsal seta. dm-Cu lacking or largely incomplete (Fig. 14). Male cercal bases narrowly separated by a distinct medial suture (i.e., not fused) (Fig. 17) ..... *M. asetosa* Kugler
- Intra-alar setae absent. Abdomen dorsally covered with dense brilliant silver microtomentum (well visible in anterodorsal view) (Fig. 21).  $R_1$  dorsally setulose. Mid tibia without anterodorsal setae. dm-Cu present (Fig. 20). Male cercal bases fused medially (Fig. 22)..... 4
- 4  $R_{4+5}$  dorsally with fine and widely spaced setulae on much of its length. Postpedicel with a row of setae along dorsal margin (Fig. 18). Ground colour of abdominal tergites mainly dark brown but pale yellowish basally and narrowly whitish on hind margins. Mid and hind femora mainly dark-brown or blackish, except for yellowish apices. Only posterior coxa entirely pale yellow. Pleural sclerites of thorax varying in colour from brown to reddish .....  
..... *M. basilewskyi* (Peris)
- $R_{4+5}$  dorsally bare. Postpedicel without setae. Ground colour of abdominal tergites pale reddish-yellow on about basal 2/3 or more and brown in the remaining surface. Mid and hind femurs pale yellow on about basal 3/5 and pale brown on the remaining surface. All coxae yellowish. Pleural sclerites of thorax almost entirely pale reddish-yellow ..... *M. argyrivertris* (Curran)

## “*roralis*-group”

### *Melanophora chia* sp. nov.

(Figs 2–11)

**Type material.** Holotype ♂: I – Sardegna (Cagliari prov.) / Dòmus de Maria, Torre di Chia / spiaggia di Su Portu, 1 m / UTM-wgs84 32S 490072 4305296 / 5.IX.2007, hand net / D. Avesani, M. Bardiani, A. Campanaro leg. [MZUR]. Paratypes: 1 ♂, 1 ♀, same data as holotype [MZUR].

**Etymology.** From the type locality “Torre di Chia”, a noun in apposition.

**Diagnosis.** Having retained the postangular portion of M and showing a female wing membrane with a whitish, sub-distal spot, this species belongs to the *roralis*-group. It differs from the widespread *M. roralis* by the following features: i) petiole of  $R_{4+5}$  very long, 2.1–2.5 times as long as postangular section of M; ii)  $Cs_6$  at least as long as  $Cs_4$  (distinctly longer in female); iii) anterodistal edge of wing with a concavity at the intersection of 4<sup>th</sup> and 6<sup>th</sup> costal sections, very pronounced in female, just visible in male; iv) female head and thorax mainly yellow in ground colour; v) male cerci, in posterior view, very narrow; basally not enlarged (Fig. 11).

#### **Description.**

**Male** (measurements in square brackets refer to the paratype):

Body length. 3.3 mm.

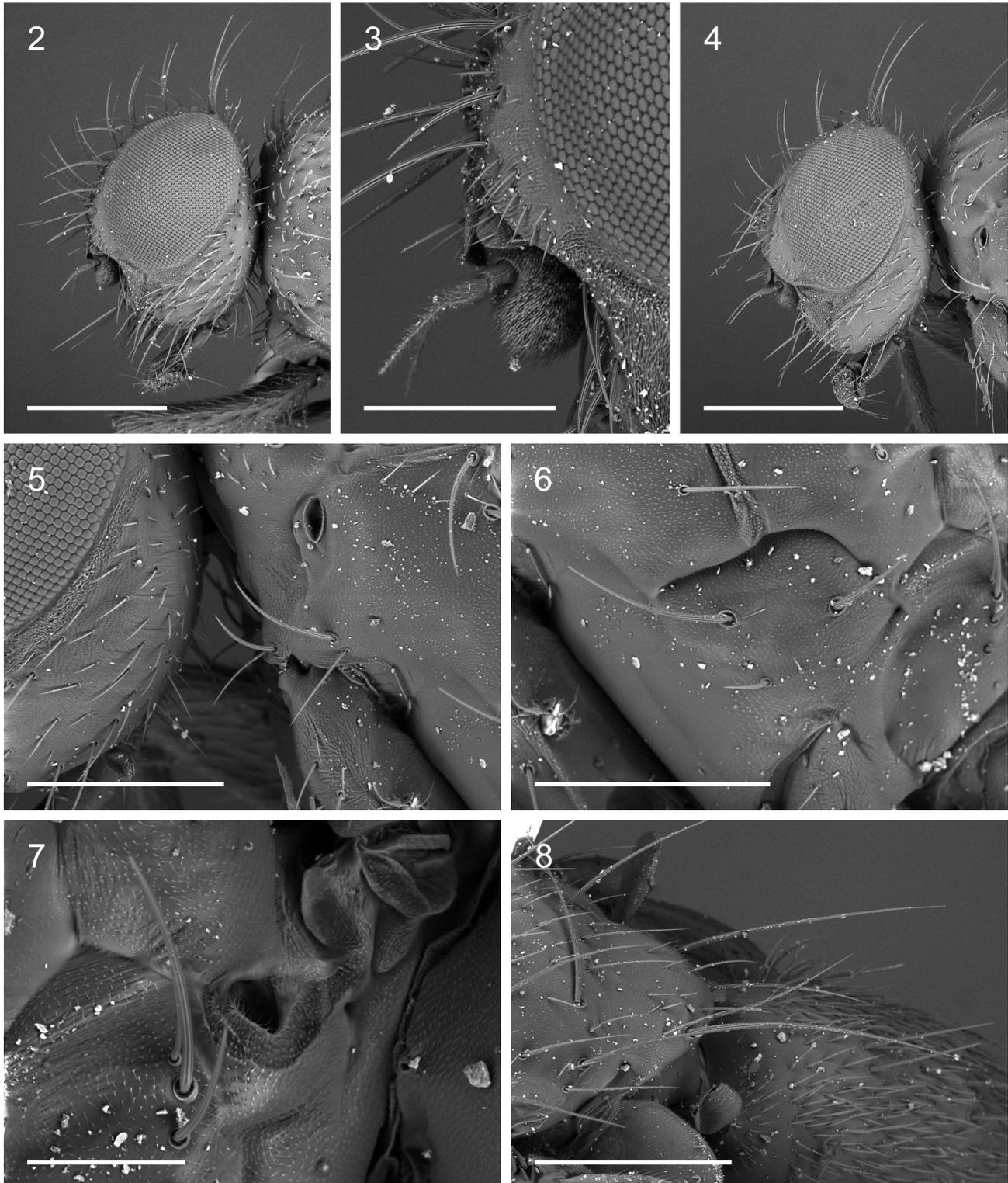
Colour. Head predominantly black, without microtomentum; frontal vitta brown; palpus and prementum black; antenna entirely black. Thorax and abdomen shiny black, without microtomentum. Legs black. Halter with black knob and brownish-orange stem. Upper and lower calypteres brownish infuscated. Wing membrane evenly brownish, but darker anterobasally.

Head (Figs 2–4). Compound eye bare. Arista thickened only at base, covered with microtrichia at most as long as its maximum diameter. First and second aristomeres not elongated. Postpedicel 1.0–[1.2] times as long as pedicel. Frons at its narrowest point 1.1 times as wide as eye in dorsal view. Ocellar setae well developed, proclinate and divergent. Medial vertical seta strong, reclinate. Lateral vertical seta well developed, about 0.7 times as long as medial vertical seta. One strong reclinate upper orbital seta. Three to 5 proclinate orbital setae. Seven to 10 frontal setae descending anteroventrally to level of proximal edge of pedicel; two dorsalmost pairs of frontal setae reclinate. Parafacial with some proclinate, fine setulae on dorsal half. Parafacial, at its narrowest point, about as wide as postpedicel (lateral view). Face and lower facial margin not visible in lateral view. Vibrissa well developed. Vibrissal angle receding. Facial ridge strongly concave, with robust, decumbent setulae on ventral half. Genal dilation well developed, covered with stout setulae. Gena in profile about 0.3 times as high as eye. Postocular setae short. Occiput slightly convex, covered with black setulae. Prementum about 2.5–3.5 times as long as wide. Oral cavity oval. Palpus subcylindrical with some setulae on distal half.

Thorax (Figs 5–8). Prosternum and proepisternal depression bare. Anteroventral proepisternal seta well developed and oriented anteroventrally. Ventral proepimeral seta oriented anteroventrally. Postpronotum with 2 strong setae. Scutum with 0–1 + 1–2 acrostichal setae, 2–3 + 3 dorsocentral, 0 + 2 intra-alar and 1 + 1 supra-alar setae (first postsutural supra-alar seta absent); 1 posthumeral, 2 well developed notopleural setae. Anatergite bare. Two strong dorsal katepisternal setae sub-equal in length and thickness, plus a smaller additional one ventrally. One short anepimeral seta. Katepimeron bare. Scutellum with 3 pairs of marginal setae: basal pair very short and weak (at most 1/4 of subapicals) sometimes indistinct; subapicals long, robust and slightly divergent; apical pair crossed and horizontal, about 2/3 as long as subapical pair. One pair of short discal scutellar setae, in subapical position.

Wing (Figs 9, 10). Costal spine not or very slightly differentiated from costal spinulae. Costal segment  $Cs_6$  at least as long as  $Cs_4$ . Costal vein with a just visible concavity at level of  $R_{4+5}$ . Base of  $R_{4+5}$  with 1, relatively long, setula dorsally. Section of M between dm-Cu and bend of M 3.1–[3.5] times as long as section between dm-Cu and r-m. Cell  $r_{4+5}$  distinctly petiolate, petiole [2.1]–2.5 times as long as postangular portion of M.

Abdomen. Mid-dorsal depression on syntergite 1+2 confined to anterior third of that segment. Syntergite 1+2 and tergite 3 with 1 pair of median marginal setae and 1 pair of lateral marginals. Tergites 4 and 5 each with a row of marginal setae.



**FIGURES 2–8.** *Melanophora chia* sp. nov. **2.** Head in lateral view (♂, holotype), scale bar: 0.5 mm. **3.** Detail of antenna and parafacial in lateral view (♂, holotype), scale bar: 0.2 mm. **4.** Head in lateral view (♀, paratype), scale bar: 0.5 mm. **5.** Back of head and anterior third of thorax in lateral view (♀, paratype), scale bar: 0.3 mm. **6.** Katepisternum in lateral view (♀, paratype), scale bar: 0.3 mm. **7.** Left metathoracic spiracle (♀, paratype), scale bar: 0.1 mm. **8.** Scutellum in laterodorsal view (♂, holotype), scale bar: 0.5 mm.

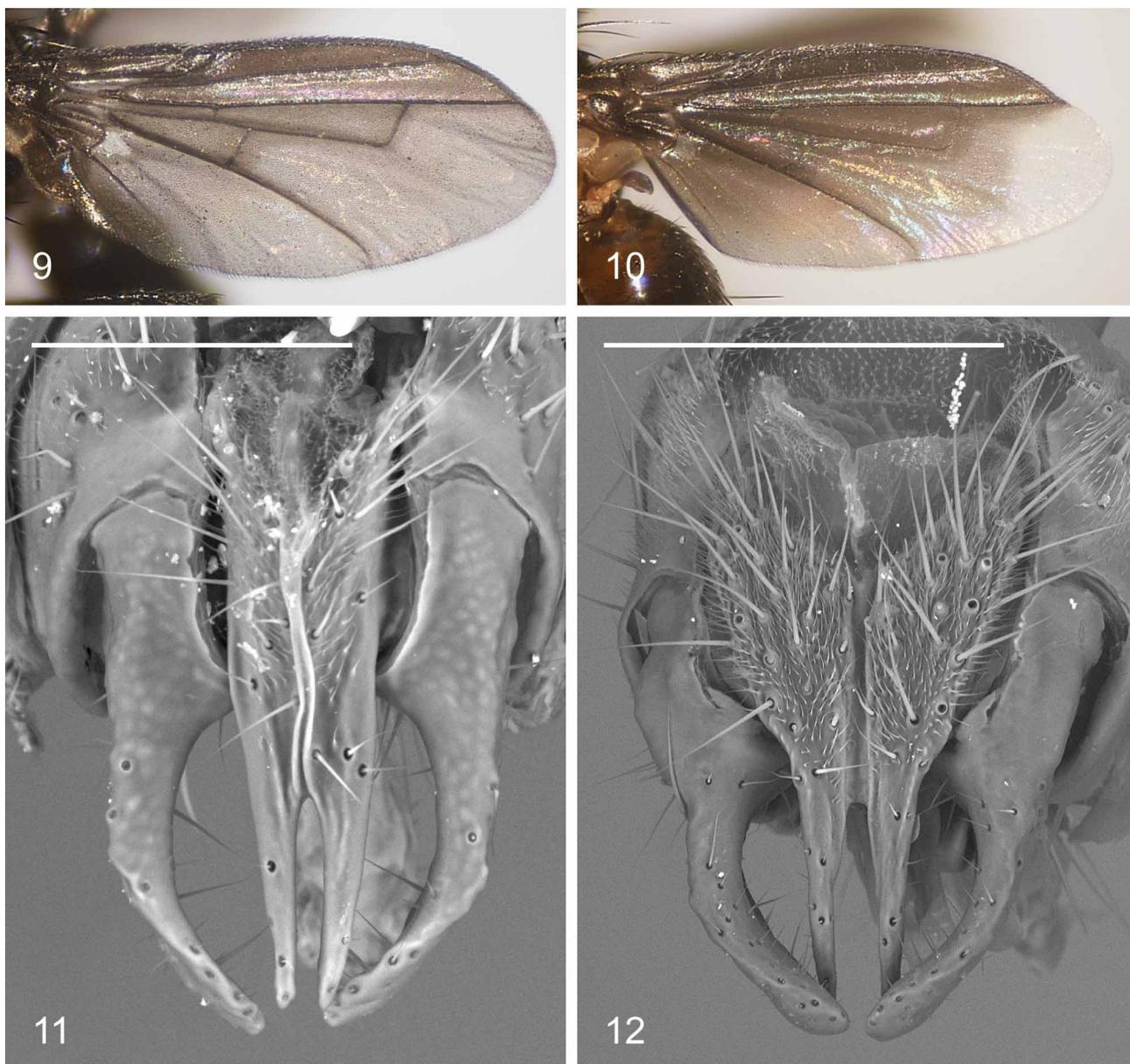
Male terminalia (Fig. 11). Cerci, in posterior view, very narrow; basally not or very slightly enlarged.

**Female** differs from male as follows:

Body length. 3.5 mm.

Colour. Frontal vitta light brown; gena, lower part of parafacial and occipital region yellow; vibrissal angle, dorsal half of parafacial, fronto-orbital plate, vertex, antenna, palpus and prementum black. Pleural sclerites, notopleuron, postpronotal lobes, as well as a wide medial vitta on scutum yellow; scutum, between dorsocentral and intra-alar rows black to dark brown; scutellum entirely black. Legs with coxa and trochanter orange-yellow and tibia, femur and tarsus black. Halter with black knob and orange-yellow stem. Lower calypter only slightly infuscated and upper calypter hyaline. Wing infuscated but with a whitish spot at the tip. Abdomen entirely black, except for anterior half of syntergite 1+2 and sides of tergite 3 that are brownish-orange.

Head. Arista bare.



**FIGURES 9–12.** *Melanophora* spp. **9–10.** Wing of *Melanophora chia* sp. nov. **9.** ♂, holotype. **10.** ♀, paratype. **11–12.** Epandrial complex in posterior view. **11.** *Melanophora chia* sp. nov. (♂, paratype), scale bar: 0.1 mm. **12.** *Melanophora roralis* (Linnaeus) (♂, Sardinia), scale bar: 0.2 mm.

Wing. Section of M between dm-Cu and bend of M 3.6 times as long as section between dm-Cu and r-m. Membrane largely brownish with a whitish spot posterodistally (Fig. 10).

Abdomen. Syntergite 1+2 and tergite 3 without lateral marginal setae.

**Distribution.** Italy (Sardinia).

### ***Melanophora roralis* (Linnaeus, 1758)**

(Fig. 12)

*Musca roralis* Linnaeus, 1758: 597. Type locality: "Europa".

**Material examined.** Numerous males and females in MZUR and ZMUC.

**References.** Herting 1961: 32; Crosskey 1977: 51; Kugler 1978: 70, 79; Crosskey 1980: 819; Herting 1993: 116.

**Description.** See Crosskey (1977).

**Distribution.** Europe (including Sicily and Sardinia), North Africa, Israel, Cape Verde Islands (introduced to eastern North America and South America).

### **"asetosa-group"**

### ***Melanophora asetosa* Kugler, 1978**

(Figs 13–17)

*Melanophora asetosa* Kugler, 1978: 70, 78. Type locality: Yeruhan (Negev), Israel.

**Material examined.** 1 ♂, Israel: 'Enot Qane, 31.i.1995, A. Freidberg leg. (TAU). 1 ♂, Israel, Zomet Mash'abbim, 11.vii.2008, I. Renan leg. (TAU). 1 ♂, Yeroham, 20.iv.1992, A. Freidberg leg. (TAU). 1 ♀, Israel, Ein-Mot, 21.ix.1983, leg. Nussbaum (TAU).

**References.** Kugler 1978: 78; Pape 1986: 24.

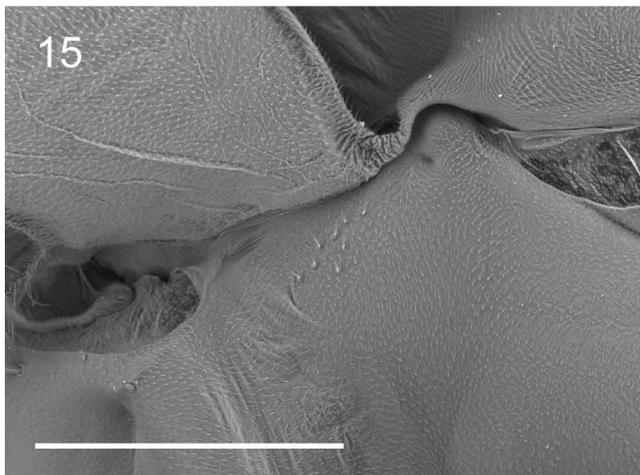
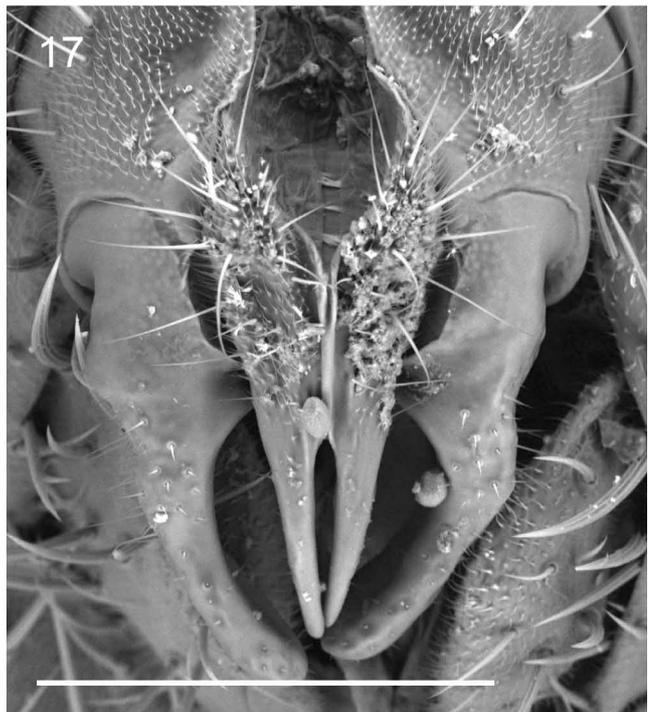
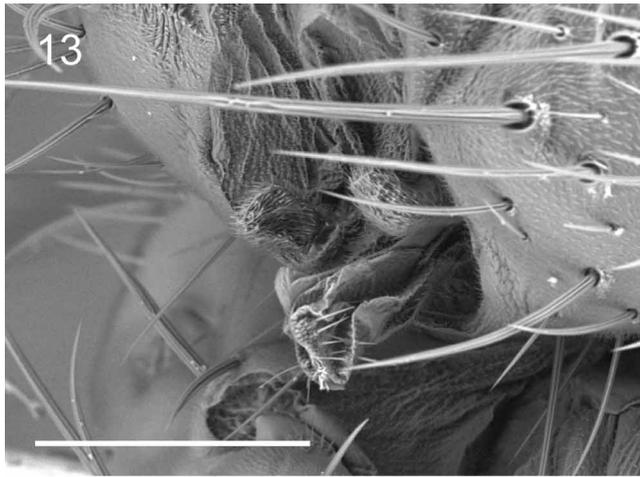
**Description.**

**Male:**

Body length. 3.7–5.0 mm.

Colour. Head predominantly brownish-black, covered with brownish microtomentum; frontal vitta reddish-brown; palpus and prementum black; pedicel basally brown shading into yellowish distally; postpedicel dark brown. Thorax blackish-brown. Abdomen shiny brown, without microtomentum (Fig. 16). Legs brownish-black. Halter with black knob and brownish-orange stem. Upper and lower calypteres brownish infuscated. Wing membrane evenly brownish (Fig. 14).

Head (Fig. 13). Compound eye bare. Arista thickened only at base, covered with microtrichia at most as long as its maximum diameter. First aristomere shorter than wide; second aristomere about 1.5 times as long as wide. Postpedicel at most as long as pedicel. Frons at its narrowest point 1.6 times as wide as eye in dorsal view. Ocellar setae shorter than upper reclinate orbital seta, proclinate and divergent. Medial vertical seta strong, convergent and reclinate. Lateral vertical seta well developed. One reclinate upper orbital seta. Five or 6 proclinate orbital setae. Eight or 9 frontal setae descending anteroventrally to level of proximal edge of pedicel; three dorsalmost pairs of frontal setae reclinate. Parafacial with some proclinate, fine setulae on dorsal half. Parafacial, at its narrowest point, about as wide as postpedicel or slightly more (lateral view). Face and lower facial margin not visible in lateral view. Vibrissa well developed. Vibrissal angle receding. Facial ridge strongly concave, with a few robust, decumbent setulae on ventral half. Genal dilation well developed, covered with stout setulae. Gena in profile about 0.4 times as high as eye. Postocular setae short. Occiput slightly convex, covered with black setulae. Oral cavity narrow and mouthparts reduced (vestigial) (Fig. 13). Palpus very short, stout and bare (Fig. 13).



**FIGURES 13–17.** *Melanophora asetosa* (Kugler) (♂, Israel). **13.** Mouthparts in lateroventral view, scale bar: 0.2 mm. **14.** Wing. **15.** Anatergite and part of left lower calypter in posterior view, scale bar: 0.3 mm. **16.** Abdomen in dorsal view. **17.** Epandrial complex in posterior view, scale bar: 0.2 mm.

Thorax (Fig. 15). Prosternum and proepisternal depression bare. Anteroventral proepisternal seta well developed and oriented anteroventrally. Ventral proepimeral seta oriented anteriorly. Postpronotum with 2 strong setae. Scutum with 0–3 + 0–5 acrostichal setae, 1–3 + 3 dorsocentral, 0 + 2 intra-alar and 1 + 1 supra-alar setae (first postsutural supra-alar seta absent); 1 posthumeral, 2 well developed notopleural setae. Anatergite with a few thin, erected setulae just below lower calypter (Fig. 15). Two dorsal katepisternal setae

sub-equal in length and thickness. One short anepimeral seta. Katepimeron bare. Scutellum with 1 pair of sub-parallel marginal setae (subapical). One pair of short discal scutellar setae.

Wing (Fig. 14). Costal spine not differentiated from costal spinulae. Costal segment  $Cs_6$  distinctly shorter than  $Cs_4$ . Base of  $R_{4+5}$  with 1 setula dorsally. Postangular portion of M lacking (M vein ends on the membrane about where the bend of M should be). Vein dm-Cu lacking.

Abdomen (Fig. 16). Mid-dorsal depression on syntergite 1+2 confined to anterior fourth of that segment. Syntergite 1+2 and tergite 3 without median marginal setae but with 1 or 2 pairs of lateral marginals. Tergite 4 and 5 each with a row of marginal setae.

Male terminalia (Fig. 17). Cercal bases, in posterior view, enlarged and not fused medially.

**Female.** See Kugler (1978).

**Distribution.** Israel.

### “*argyrivertris*-group”

#### *Melanophora argyrivertris* (Curran, 1929) comb. nov.

*Bequaertiana argyrivertris* Curran, 1929: 15. Type locality: Du River, Liberia.

**Material examined.** [None.]

**References.** Crosskey 1977: 55 (as *Bequaertiana*) (and references therein); Pape 1986: 24 (as *Bequaertiana*).

**Description.** See Crosskey (1977).

**Distribution.** Liberia (cf. Crosskey 1977; Crosskey 1980, as *Bequaertiana*).

#### *Melanophora basilewskyi* (Peris, 1957) comb. nov.

(Figs 18–22)

*Bequaertiana basilewskyi* Peris, 1957: 136. Type locality: Ruhengeri, Rwanda.

**Material examined.** 3 ♂♂, Kenya, Mt. Elgon Lodge, 1–6.XI.1983, Malaise trap, A. Freidberg [TAU] (first Kenyan record).

**References.** Crosskey 1977: 56 (as *Bequaertiana*) (and references therein); Crosskey 1980: 819 (as *Bequaertiana*); Pape 1986: 24 (as *Bequaertiana*).

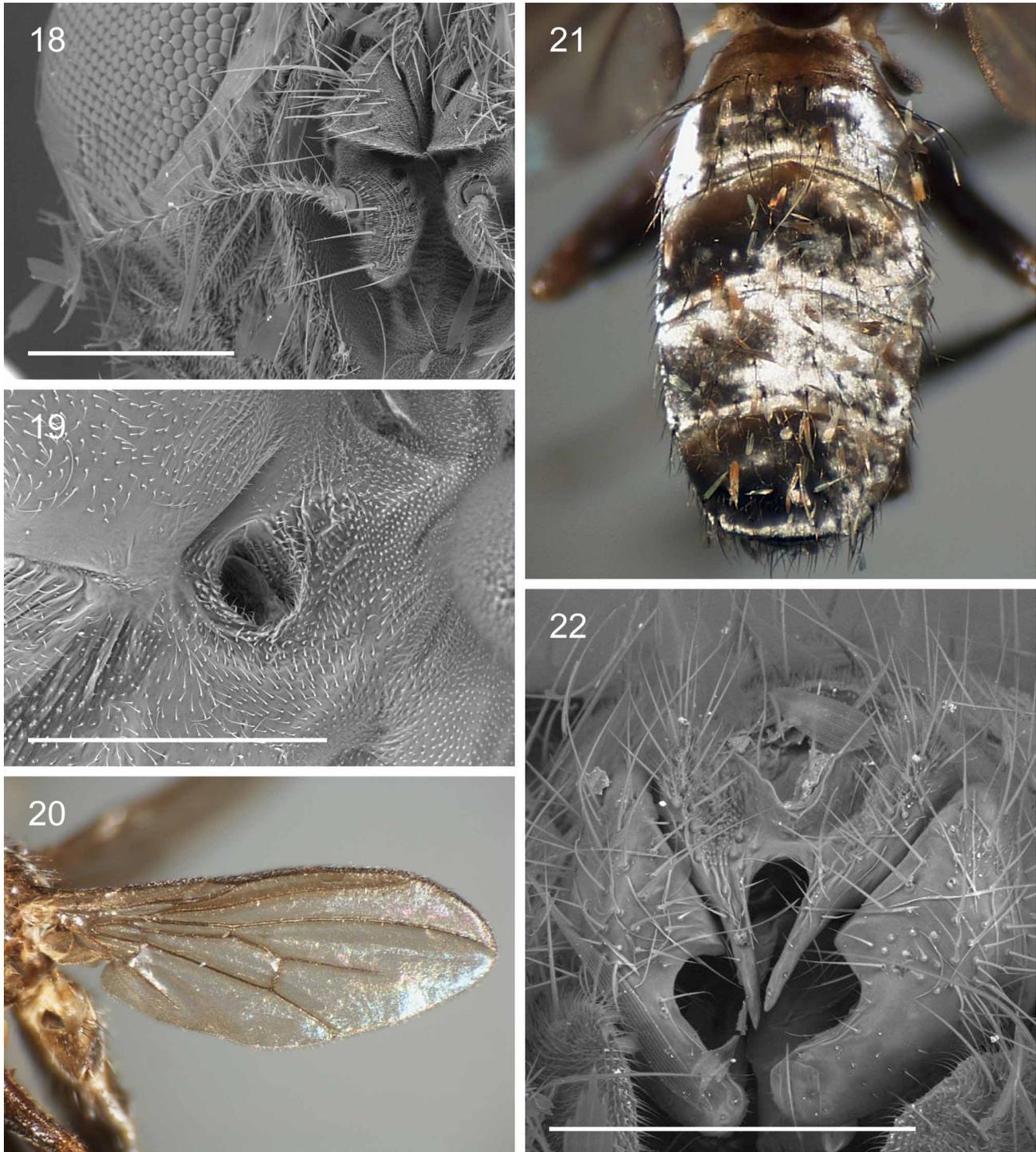
**Description.** See Crosskey (1977).

**Distribution.** Democratic Republic of Congo, Uganda, Rwanda, Kenya.

### Discussion

Pape (1986) first discussed the monophyly of the clade *Melanophora* + *Bequaertiana* based on adult characters, stressing that *Melanophora* (then including *M. roralis* and *M. asetosa*) could be paraphyletic with respect to *Bequaertiana*. However, no synonymy was proposed at the time as the lack of males of *M. asetosa* (described here for the first time) and the lack of females of *Bequaertiana* made a decision premature.

Our analysis, performed using several of the characters already coded by Pape (1986) plus additional ones, supports the monophyly of the re-defined *Melanophora* (formerly *Melanophora* + *Bequaertiana*) (Fig. 1). The monophyly of the genus is corroborated by the following three autapomorphies: (0:2) arista with bottlebrush-like trichia in male and usually bare in female, (3:1) female with several [3–7] proclinate orbital setae, and (7:1) dorsalmost pairs of frontal setae sub-parallel.



**FIGURES 18–22.** *Melanophora basilewskyi* (Peris) (♂, Kenya). **18.** Right antenna in frontal view, scale bar: 0.3 mm. **19.** Left metathoracic spiracle, scale bar: 0.2 mm. **20.** Wing. **21.** Abdomen in dorsal view. **22.** Epandrial complex in posterior view, scale bar: 0.3 mm.

Even if not yet confirmed for *M. argyrivertris* and *M. basilewskyi* (for which females are still unknown), states 0:2 and 3:1 seem to be strong autapomorphies supporting the monophyly of *Melanophora*, given that no other members of the Rhinophoridae have males with such trichosity on the arista and females with more than two proclinate orbital setae. The inclination and orientation of the dorsalmost pairs of frontal setae appears in this analysis as another autapomorphy, but the apomorphic state shown by *Melanophora* is shared with

specimens of an unidentified genus from Namibia that may be unrelated to *Melanophora* (Cerretti/Pape, unpublished data), thereby making this feature homoplastic.

As for relationships between species of *Melanophora*, three well corroborated species groups can be identified (Fig. 1).

The “*roralis*-group” (*M. roralis* + *M. chia* sp. nov.) is supported by the whitish wing tip in the female (19:1). This state, already mentioned by Pape (1986) as characteristic of *M. roralis*, is unique within the Rhinophoridae.

*Melanophora asetosa*, *M. argyrivertris* and *M. basilewskyi* share the following four apomorphies: mouthparts strongly reduced (8:1), apical scutellar setae absent (14:1), postangular section of M absent (22:1), and abdominal tergite 3 without median marginal setae (25:1). States 8:1 and 25:1 are unique within the Rhinophoridae while the absence of the postangular section of M independently occurs also in *Oplisa aterrima* (Strobl), which is clearly unrelated to *Melanophora* (see Pape 1986). Noteworthy, the sister-group relationship between *Melanophora asetosa* and the two Afrotropical species *M. argyrivertris* and *M. basilewskyi* is highly corroborated (Bremer support of four). This means that *Melanophora roralis* and *M. asetosa* cannot be considered congeneric without also including the morphologically quite deviating Afrotropical species, confirming the paraphyly of the former concept of *Melanophora* (cf. Pape 1986; Pape 1998). Any classification seeking to acknowledge the certainly highly apomorphic appearance of these Afrotropical species, which could be considered formally as belonging to a separate subgenus (*Bequaertiana*) or informally as a species-group (like in the present paper), would have to treat *M. asetosa* similarly.

*Melanophora asetosa* is characterized by the absence of crossvein dm-Cu, which is unquestionably an autapomorphy representing a very rare condition in the Oestroidea. The monophyly of *Melanophora argyrivertris* and *M. basilewskyi* (the “*argyrivertris*-group”) has been discussed by Crosskey (1977) and Pape (1986) and is here confirmed and well corroborated by the absence of intra-alar setae (13:1), the reduced metathoracic spiracular lappets (16:0), the reduced leg chaetotaxy (17:1), the dense, silvery abdominal microtomentum (24:1), and the medial fusion of the male cerci (28:1).

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**APPENDIX 1.** Characters and character states and the resulting matrix used in the phylogenetic analysis. When two or more states occur in a single terminal taxon, these are given in brackets; unknown and inapplicable states are coded as question marks.

- 0 Arista: (0) bare or apparently so in both sexes; (1) pubescent (not bottlebrush-like) in both sexes; (2) with bottlebrush-like trichia in male and usually bare in female.
- 1 Lunula: (0) bare; (1) with setae.
- 2 Male proclinate orbital setae: (0) absent; (1) present.
- 3 Female proclinate orbital setae: (0) two; (1) several (3–7).
- 4 Facial profile: (0) vibrissal angle not receding, distinctly in front of anterior margin of compound eye; (1) vibrissal angle receding.
- 5 Compound eye: (0) not enlarged (gena and parafacial distinct); (1) very enlarged (gena and parafacial almost obliterated).
- 6 Parafacial: (0) bare or with scattered short setulae on dorsal half; (1) covered with short dense setulae; (2) with long robust proclinate setae and setulae along whole length or with at least 2–3 strong setae on ventral half.
- 7 Orientation of dorsalmost pairs of frontal setae: (0) converging in the middle and crossed; (1) sub-parallel.
- 8 Mouthparts: (0) unmodified (Figs 2, 4); (1) strongly reduced (vestigial) (Fig. 13).
- 9 Anteroventral seta of proepisternal lobe: (0) well developed, directed dorsally; (1) well developed, directed antero-ventrally (Fig. 5); (2) absent or hair-like.
- 10 Ventral proepimeral seta: (0) well developed, directed dorsally; (1) well developed, directed anteroventrally (Fig. 5); (2) absent or hair-like.
- 11 Postpronotal chaetotaxy: (0) three setae standing in line or nearly so; (1) three strong setae forming an almost right-angled triangle.
- 12 First postsutural supra-alar seta: (0) present and well developed; (1) absent or very short and hair-like.
- 13 Intra-alar setae: (0) present [0–1 + 2(3)]; (1) absent.
- 14 Apical scutellar setae: (0) present (Fig. 8); (1) absent.
- 15 Katepimeron: (0) pubescent and with at least one seta anteriorly; (1) entirely bare.
- 16 Anterior and posterior metathoracic spiracular lappets: (0) practically absent (Fig. 19); (1) small, sub-equal in size and directed outwards (Fig. 7); (2) unequal in size (anterior one distinctly larger) and both lappets closing the spiracle like an operculum.
- 17 Leg chaetotaxy: (0) not particularly modified; (1) reduced and with almost no strong setae.
- 18 Shape of lower calypter: (0) semicircular; (1) tongue-shaped.
- 19 Pattern of female wing membrane: (0) without any whitish spot posterodistally; (1) with a distinct whitish spot posterodistally (Fig. 10).
- 20 Sixth costal section ( $Cs_6$ ): (0) indistinct (= M, or petiole of  $r_{4+5}$ , ends at the distal wing tip); (1) well developed.
- 21 Wing cell  $r_{4+5}$ : (0) open at wing margin; (1) closed or short petiolate; (2) long petiolate.
- 22 Postangular section of M: (0) present (Figs 9–10); (1) absent (Figs 14, 20).
- 23 dm-Cu: (0) present; (1) absent (Fig. 14).
- 24 Male abdominal microtomentum: (0) not particularly dense and silvery; (1) dense and silvery (Fig. 21).
- 25 Median marginal setae on abdominal tergite 3: (0) present; (1) absent or very short and recumbent.
- 26 Marginal setae on tergite 4: (0) a regular row of more or less erect marginal setae; (1) marginal setae absent or not differentiated from general abdominal setulae.
- 27 Shape of male sternite 5: (0) posterior margin with a median deep cleft and with a more or less visible transverse membranous stripe; (1) posterior margin straight or gently concave.
- 28 Male cercal bases: (0) not fused medially (Figs 11–12, 17); (1) at least partly fused medially (Fig. 22).

- 29 Articulation between processus longi and surstylus: (0) articulated, not fused; (1) firmly fused.
- 30 Dorsal sclerotization of distiphallus: (0) divided into a pair of dorsolateral processes curved anteriorly; (1) divided into a pair of dorsolateral processes not curved anteriorly; (2) fused into a single dorsomedian sclerotization; (3) fused into a single, well developed dorsomedian sclerotization ending with a membranous “flag” (*cf.* Tschorsnig 1985).
- 31 Ventral sclerotisation: (0) not interrupted, running from the ventral plate to tip of phallus; (1) interrupted proximally and not connected to ventral plate.
- 32 Acrophallus: (0) simple, unmodified; (1) distinctly tripartite (or trilobate).
- 33 Female terminalia: (0) long and telescopic; (1) shortened.

Data matrix	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33			
<i>C. vomitoria</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>M. roralis</i>	2	0	1	1	1	0	0	1	0	1	1	0	1	0	0	1	0	0	1	1	1	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1
<i>M. chia</i>	2	0	1	1	1	0	0	1	0	1	1	0	1	0	0	1	0	0	1	1	1	2	0	0	0	0	0	0	0	0	0	2	0	0	1		
<i>M. asetosa</i>	2	0	1	1	1	0	0	1	1	1	1	0	1	0	1	1	0	0	1	0	1	?	1	1	0	1	0	0	0	0	2	0	0	1			
<i>M. argyriventris</i>	?	0	1	?	1	0	0	1	1	?	?	0	1	1	1	1	1	1	1	1	?	1	?	1	0	1	1	1	0	1	0	2	0	0	?		
<i>M. basilewskyi</i>	?	0	1	?	1	0	0	1	1	1	2	1	0	1	1	1	1	1	1	1	?	1	?	1	0	1	1	1	0	1	0	2	0	0	?		
<i>V. milichioides</i>	0	0	1	?	1	1	1	0	0	2	1	0	1	0	0	1	0	0	1	?	0	0	0	0	?	0	0	0	0	1	3	0	1	?			
<i>Pa. nubilipennis</i>	0	0	1	0	1	0	0	0	0	0	1	1	0	1	0	0	1	0	0	1	0	1	2	0	0	0	0	0	1	0	0	1	0	0	1		
<i>Ph. angustifrons</i>	0	1	0	0	0	0	2	0	0	2	2	0	0	0	0	0	0	0	1	0	1	2	0	0	0	0	0	0	0	0	0	0	1	0	0		
<i>Ph. adolescens</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0		
<i>S. signata</i>	0	0	1	0	0	0	2	0	0	1	1	1	0	0	1	0	0	1	0	1	2	0	0	0	0	0	0	0	0	0	1	3	0	1	0		
<i>S. deceptor</i>	0	0	0	0	0	0	2	0	0	1	1	1	1	0	0	1	0	0	1	0	1	2	0	0	0	0	0	0	0	1	3	0	1	0	0		