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Costal vein chaetotaxy, a neglected character source in Fanniidae and Muscidae (Diptera: Calyptratae)

Verner MICHELSEN

Natural History Museum of Denmark, University of Copenhagen, Denmark.
Email: vmichelsen@snm.ku.dk

urn:lsid:zoobank.org:author:9BD4846E-F4D0-4DB2-A567-FAF0A58B6D98

Abstract. The present study examines whether the chaetotaxy of the costal vein in the calyptrate families Fanniidae and Muscidae deserves more attention in phylogenetic and taxonomic contexts. An overview of the macrotrichia and their arrangement on wing vein C is given. Special attention is given to the presence/absence of ventral and dorsal setulae on the costal sectors CS1–3. This is described as one variable character (**A**) with nine states (**A0–A8**). Specimens of both sexes (when possible) of each species belonging to 4 of a total of 5 fanniid genera and 115 of a total of 179 muscid genus-group taxa were examined and scored for character **A**. It was found that the presumed ancestral state of character **A** differs between the two families. It is further shown that the main transformational trend in character **A** in Muscidae has been bi-directional, leading either to the loss of ventral setulae or the gain of dorsal setulae. The utility of character **A** in the Fanniidae and Muscidae is many-sided and involves taxa ranging from species to family. It is concluded that character **A** and other aspects of costal chaetotaxy deserve more attention in morphology-based studies of calyptrate flies.

Keywords. Macrotrichia, setulae, spinules, vein C, morphology, taxonomy, phylogeny.

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Introduction

The costal vein C (Fig. 1A–B) constitutes the first longitudinal vein and the anterior edge of the wing in Diptera. As documented by Hackman & Väisänen (1985), the chaetotaxy of vein C in Diptera embodies a suite of variable characters of potential value in taxonomy and phylogeny. Still, this chaetotaxy has generated little attention in most groups of Diptera, including the major radiation known as the Calyptratae. Only the spines at the subcostal break, or more extensively on vein C, are regularly mentioned in taxonomic texts in case these are notably enlarged.

Ongoing attempts to construct a practical key to the genera and species of the calyptrate family Anthomyiidae of NW Europe based primarily on external characters made me aware of the utitily of characters from the chaetotaxy of vein C. One variable character in particular, viz to what extent the ventral and dorsal surfaces of vein C are bare or setulose, turned out to be a valuable source of reliable states worth incorporating in identification keys, diagnoses and descriptions. My experience with the

Anthomyiidae made me curious to find out whether the same character has been unjustly ignored in other calyptrate families. The present study attempts to answer this question in the calyptrate families Fanniidae and Muscidae.

The wing of calyptrate Diptera is as a rule covered on both sides in dense, hair-like microtrichia representing simple cuticular outgrowths (Fig. 1A). In addition, the wing veins are, to a varying extent, supplied with innervated macrotrichia of different kinds, but clearly dominated by mechano-sensory sensilla in the shape of setulae, spinules and spines, depending on their length and strength (Fig. 1A; se, sp). These are invariably present in dense rows on vein C and frequently also in small groups or loose rows on some of the other veins. Campaniform sensilla (Fig. 1A; cs), detectors of cuticular stress, are found isolated or clustered on certain veins other than vein C in the basal part of the wing (Gnatzy *et al*. 1987). Instead, vein C has a loose dorsal row of fine, hair-like chemo-sensory macrotrichia (Figs 1A, 2D; gs). These are no doubt homologous with the gustatory costal sensilla in *Drosophila* studied by Valmalette *et al*. (2015) and Raad *et al*. (2016).

Material and methods

Specimens examined

The results of the present paper are based primarily on the examination of specimens from the large collections of dry-mounted Fanniidae and Muscidae in the Natural History Museum of Denmark, Copenhagen, Denmark (NHMD), supplemented with species of Fanniidae from the Australian National Insect Collection, Canberra, Australia (ANIC).

Illustrations

Detached wings were mounted temporarily in 70% EtOH on glass slides with cover slips. The photos were taken with the use of a Leica MZ 16A microscope with a mounted Leica DFC420 camera. The software used was Leica Application Suite ver. 4, with built-in stacking facilities. Regarding the photos, wings pointing to the right are dorsal views, those pointing to the left are ventral views.

Costal chaetotaxy

Vein C in calyptrate flies (other than Hippoboscoidea, Scathophagidae and Oestridae) is nearly always armed with two parallel anterior rows of alternating spinules and setulae extending from the humeral break to well beyond the tip of vein R_{4+5} (Fig. 1B). Both rows gradually diminish in strength towards the apex of the wing concomitant with the diminishing strength of vein C. This spinule-setula pattern, almost confined to calyptrate families, was denoted as costal chaetotaxy "Type C" by Hackman & Väisänen (1985). Frequently, the spinules at the subcostal break are to a varying extent enlarged and referred to as spines (e.g., Fig. 13A–B). In addition – and this is the main issue of the present study – vein C is bare or to a varying extent setulose on the ventral and dorsal surfaces behind the lower and upper spinule-setula rows. In order to describe this variation it is convenient to divide vein C into sectors determined by the costal breaks and terminations of veins Sc, R_1, R_{2+3} and R_{4+5} in vein C. The costal sectors CS1–4 (Fig. 1A) are presently delimited as follows:

CS1 by the humeral and subcostal breaks
CS2 by the subcostal break and the termination of vein R_1 in vein C
CS3 by the terminations of veins R_1 and R_{2+3} in vein C
CS4 by the terminations of veins R_{2+3} and R_{4+5} in vein C

The basal part of vein C, delimited by the costagial and humeral breaks, is not counted here as a costal sector because of its deviating, stable coverage of uniform longish setulae.

The observed variation in the development of setulae on the ventral and dorsal surfaces of vein C among Fanniidae and Muscidae is described below as a single multi-state character (**A**). This follows from my observation that dorsal costal setulae in fanniid and muscid species are only found in combination with a full coverage of ventral costal setulae.

Character **A** is divided into nine states as defined below. Notice that states **A0–3** all agree with **A4** in the absence of dorsal setulae on vein C and states **A5–8** all agree with **A4** in being extensively setulose ventrally on vein C.

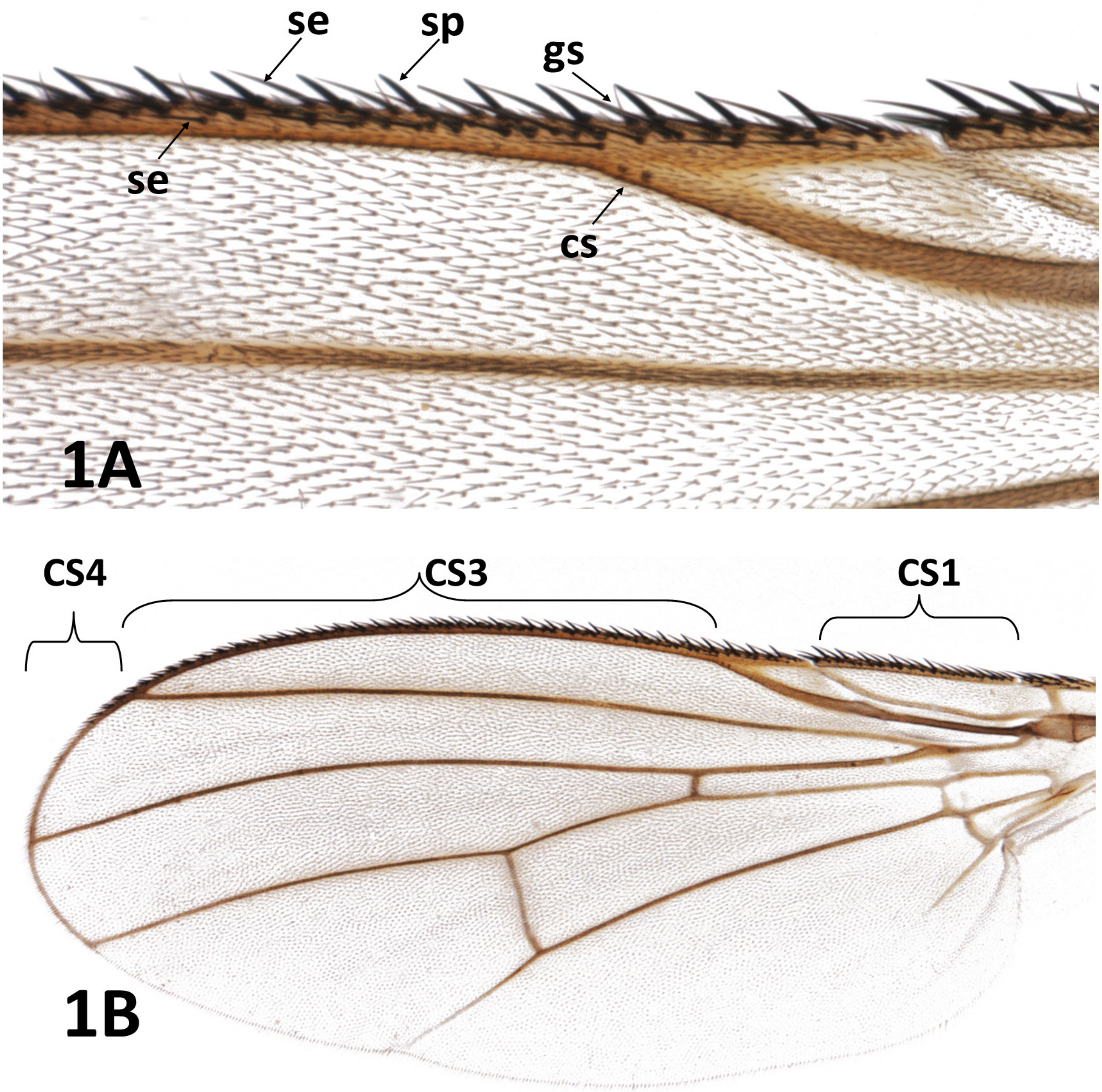

Fig. 1. *Coenosia pudurosa* Collin, 1953, ♀. **A**. Detail of wing, ventral view, showing different kinds of macrotrichia: cs = campaniform sensillum; gs = gustatory sensillum; se = setula; sp = spinule. **B**. Wing, ventral view showing costal sectors 1–4: CS = costal sector.

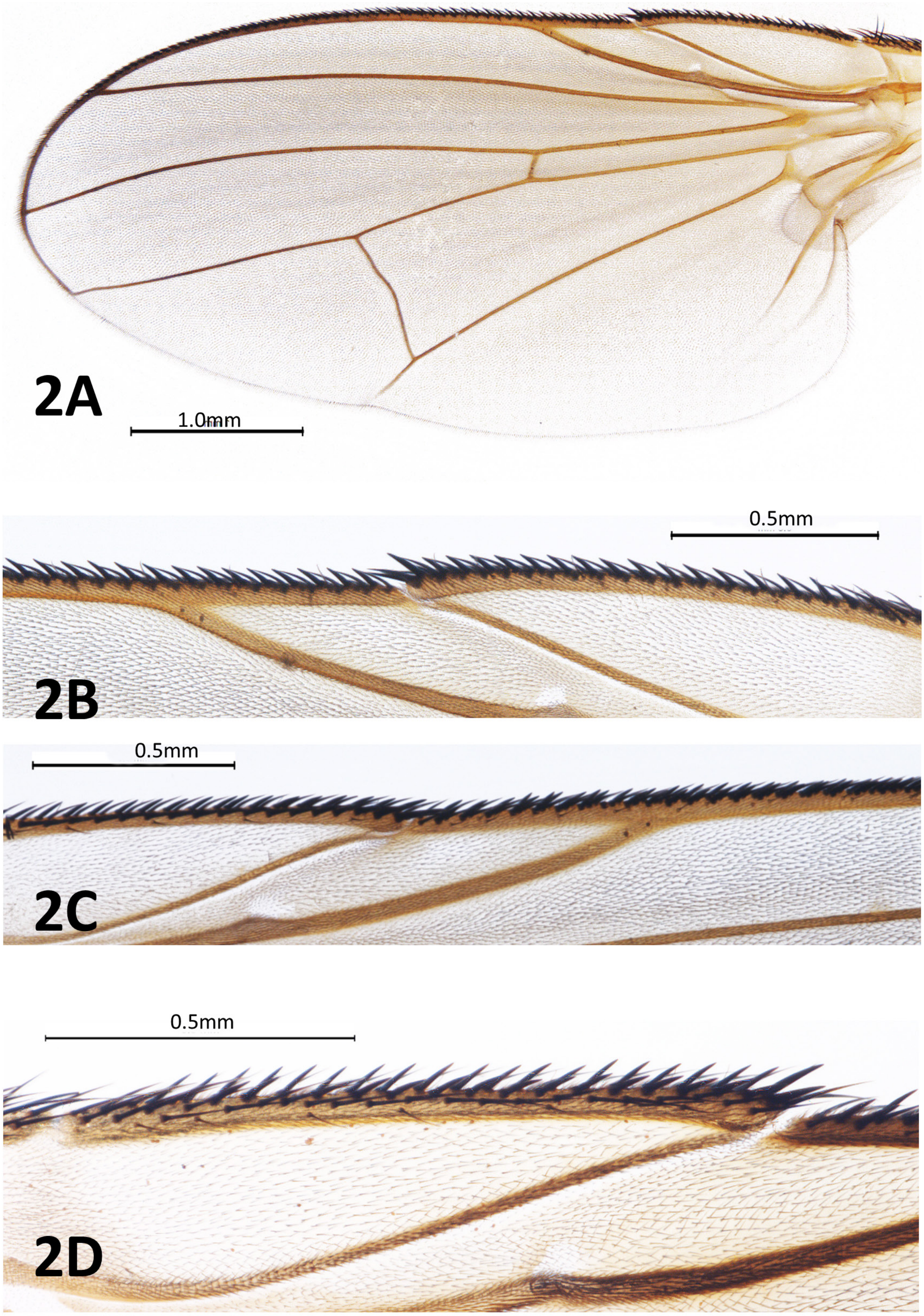

Fig. 2. ♀♀ of Fanniidae Schnabel & Dziecicki, 1911. **A**. *Fannia fuscula* (Fallén, 1825), wing, ventral view. **B**. Same, detail of wing showing CS1–3, ventral view. **C**. Same, detail of wing showing CS1–3, dorsal view. **D**. *Piezura pardalina* Rondani, 1866, detail of wing showing CS1 in dorsal view.

A0 Vein C without ventral setulae on CS1–CS4, disregarding the occational presence of a few setulae at the extreme base of CS1

A1 Vein C with ventral setulae occupying less than the basal two-thirds of CS1

A2 Vein C with ventral setulae occupying all of CS1, sometimes with some irregular setulae on CS2, rarely even on the basal part of CS3

A3 Vein C with ventral setulae occupying CS2 and more than the basal half of CS3

A4 Vein C with ventral setulae occupying CS1, CS2 and more than the basal third of CS3; vein C bare or practically so dorsally on CS1–4

A5 Vein C with dorsal setulae primarily confined to the basal half or more of CS1, but sometimes with scattered setulae dispersed onto CS2

A6 Vein C with dorsal setulae primarily confined to CS2, but frequently with scattered setulae dispersed onto the adjacent costal sectors

A7 Vein C with dorsal setulae on the basal half to two-thirds of CS3, but they sometimes reach onto CS2

A8 Vein C with dorsal setulae occupying CS1, CS2 and usually more than the basal half of CS3, sometimes even extending onto the basal part of CS4

A few species have the setulae from one or both anterior spinule-setula rows of vein C displaced ventrally or dorsally relative to the spinules. This is rarely seen in species of Fanniidae and Muscidae according to my observations, but a few cases are described below. Such displaced setulae obviously do not count as 'true' ventral or dorsal setulae. Likewise, the tiny and delicate gustatory sensilla (Fig. 1A; gs) inserted in a loose row behind the upper anterior spinule-setula row should not be scored as dorsal setulae in the sense of character **A**.

Results

Class Insecta Linnaeus, 1758
Order Diptera Linnaeus, 1758
Section Schizophora Becher, 1882
Subsection Calyptratae Robineau-Desvoidy, 1830
Superfamily Muscoidea Latreille, 1802

Family **Fanniidae** Schnabl & Dziedzicki, 1911

A distinctive, modest-sized family known for ca 400 extant species currently classified in five genera (Table 1). Species belonging to four fanniid genera have presently been scored for the distribution of setulae dorsally and ventrally (character **A**) on vein C (Table 1) in agreement with the states described above.

- *Euryomma* Stein, 1899, *Fannia* Robineau-Desvoidy, 1830 (Fig. 2A–C), *Piezura* Rondani, 1844 (Fig. 2D)

All examined species are without ventral setulae behind the lower anterior row of alternating spinules and setulae of vein C (state **A0**): *Euryomma americanum* Chillcott, 1961, *E. muisca* Grisales, Wolff & de Carvalho, 2012, *E. peregrinum* (Meigen, 1826), *Fannia* (50+ spp) incl. *F. fuscula* (Fallén, 1825) (Fig. 2A–C), *Piezura graminicola* (Zetterstedt, 1846) and *P. pardalina* Rondani, 1866 (Fig. 2D).

In *Piezura graminicola* and *P. pardalina* (Fig. 2D) rows of ventral and dorsal costal setulae on CS1 represent setulae displaced from the anterior spinule-setula rows; these accordingly consist of spinules only.

Table 1 (continued on next 4 pages). Summary of vein C chaetotaxy with respect to multistate character **A** for genus-group taxa of Fanniidae Schnabel & Dziedcicki, 1911 and Muscidae Latreille, 1802. Examined genera highlighted in yellow. See 'Material and methods' for explanation of character states A0–8.

Family	Subfamily	Tribe	Genus	Character state(s)
Fanniidae			*Australofannia*	A8
Fanniidae			*Euryomma*	A0
Fanniidae			*Fannia*	A0
Fanniidae			*Piezura*	A0
Fanniidae			*Zealandofannia*	
Muscidae	Azeliinae		*Achanthiptera*	A4
Muscidae	Azeliinae		*Anthocoenosia*	
Muscidae	Azeliinae		*Australophyra*	A2
Muscidae	Azeliinae		*Azelia*	A0
Muscidae	Azeliinae		*Drymeia*	A0, [A4]
Muscidae	Azeliinae		*Huckettomyia*	A8
Muscidae	Azeliinae		*Hydrotaea*	A4, A2, A1, A0
Muscidae	Azeliinae		*Micropotamia*	
Muscidae	Azeliinae		*Neohydrotaea*	A4
Muscidae	Azeliinae		*Potamia*	A4
Muscidae	Azeliinae		*Thricops*	A4, A7, A8
Muscidae	Azeliinae		*Xestomyia*	
Muscidae	Muscinae	Muscini	*Biopyrellia*	A4
Muscidae	Muscinae	Muscini	*Curranosia*	A4
Muscidae	Muscinae	Muscini	*Dasyphora* s. str.	A4
Muscidae	Muscinae	Muscini	subgen. *Eudasyphora*	A4
Muscidae	Muscinae	Muscini	subgen. *Rypellia*	A4
Muscidae	Muscinae	Muscini	*Deltotus*	A4
Muscidae	Muscinae	Muscini	*Hennigmyia*	A4
Muscidae	Muscinae	Muscini	*Mesembrina*	A2
Muscidae	Muscinae	Muscini	*Mitroplatia*	A4
Muscidae	Muscinae	Muscini	*Morellia* s. str.	A4
Muscidae	Muscinae	Muscini	subgen. *Parapyrellia*	A4
Muscidae	Muscinae	Muscini	subgen. *Trichomorellia*	A4
Muscidae	Muscinae	Muscini	subgen. *Xenomorellia*	A4
Muscidae	Muscinae	Muscini	*Musca*	A2, A1, A0
Muscidae	Muscinae	Muscini	*Myiophaea*	A4
Muscidae	Muscinae	Muscini	*Neomyia*	A4, A2
Muscidae	Muscinae	Muscini	*Neorypellia*	A4
Muscidae	Muscinae	Muscini	*Polietes*	A4, A2
Muscidae	Muscinae	Muscini	*Polietina*	A4
Muscidae	Muscinae	Muscini	*Pyrellia*	A2, A1
Muscidae	Muscinae	Muscini	*Pyrellina*	A4
Muscidae	Muscinae	Muscini	*Sarcopromusca*	A4

Table 1 (continued).

Family	Subfamily	Tribe	Genus	Character state(s)
Muscidae	Muscinae	Muscini	*Ziminellia*	A4
Muscidae	Muscinae	Stomoxyini	*Bruceomyia*	
Muscidae	Muscinae	Stomoxyini	*Haematobia*	A4, A2
Muscidae	Muscinae	Stomoxyini	*Haematobosca*	A4, A2, A1
Muscidae	Muscinae	Stomoxyini	*Haematostoma*	
Muscidae	Muscinae	Stomoxyini	*Neivamyia*	A2
Muscidae	Muscinae	Stomoxyini	*Parastomoxys*	
Muscidae	Muscinae	Stomoxyini	*Prostomoxys*	
Muscidae	Muscinae	Stomoxyini	*Rhinomusca*	
Muscidae	Muscinae	Stomoxyini	*Stomoxys*	A4, A2
Muscidae	Muscinae	Stomoxyini	*Stygeromyia*	A0
Muscidae	Atherigoninae		*Atherigona*	A0
Muscidae	Reinwardtiinae		*Balioglutum*	
Muscidae	Reinwardtiinae		*Brachygasterina*	[A7], A8
Muscidae	Reinwardtiinae		*Callainireinwardtia*	
Muscidae	Reinwardtiinae		*Calliphoroides*	
Muscidae	Reinwardtiinae		*Chaetagenia*	
Muscidae	Reinwardtiinae		*Correntosia*	
Muscidae	Reinwardtiinae		*Dalcyella*	
Muscidae	Reinwardtiinae		*Fraserella*	
Muscidae	Reinwardtiinae		*Muscina*	A4
Muscidae	Reinwardtiinae		*Palpibracus*	A8
Muscidae	Reinwardtiinae		*Passeromyia*	A4
Muscidae	Reinwardtiinae		*Philornis*	A4
Muscidae	Reinwardtiinae		*Psilochaeta*	A8
Muscidae	Reinwardtiinae		*Reinwardtia*	
Muscidae	Reinwardtiinae		*Synthesiomyia*	A2
Muscidae	Cyrtoneurininae		*Arthurella*	A7, A8
Muscidae	Cyrtoneurininae		*Cariocamyia*	
Muscidae	Cyrtoneurininae		*Charadrella*	
Muscidae	Cyrtoneurininae		*Chortinus*	
Muscidae	Cyrtoneurininae		*Cyrtoneurina*	A4
Muscidae	Cyrtoneurininae		*Cyrtoneuropsis*	A4
Muscidae	Cyrtoneurininae		*Itatingamyia*	
Muscidae	Cyrtoneurininae		*Mulfordia*	
Muscidae	Cyrtoneurininae		*Neomuscina*	A4
Muscidae	Cyrtoneurininae		*Neomusciniopsis*	
Muscidae	Cyrtoneurininae		*Neurotrixa*	
Muscidae	Cyrtoneurininae		*Pseudoptilolepis*	A8
Muscidae	Phaoniinae	Phaoniini	*Beccimyia*	
Muscidae	Phaoniinae	Phaoniini	*Buccophaonia*	

Table 1 (continued).

Family	Subfamily	Tribe	Genus	Character state(s)
Muscidae	Phaoniinae	Phaoniini	*Chaetophaonia*	
Muscidae	Phaoniinae	Phaoniini	*Dolichophaonia*	
Muscidae	Phaoniinae	Phaoniini	*Helina*	A4 [A6, A7, A8]
Muscidae	Phaoniinae	Phaoniini	*Hennigiola*	
Muscidae	Phaoniinae	Phaoniini	*Lophosceles*	A7, A8
Muscidae	Phaoniinae	Phaoniini	*Metopomyia*	A4
Muscidae	Phaoniinae	Phaoniini	*Phaomusca*	A4
Muscidae	Phaoniinae	Phaoniini	*Phaonia*	A4, A6 , A7, A8
Muscidae	Phaoniinae	Phaoniini	*Phaonidia*	
Muscidae	Phaoniinae	Phaoniini	*Phaonina*	
Muscidae	Phaoniinae	Phaoniini	*Pictia*	A4
Muscidae	Phaoniinae	Phaoniini	*Polletella*	
Muscidae	Phaoniinae	Phaoniini	*Prohardyia*	A4
Muscidae	Phaoniinae	Phaoniini	*Rhynchomydaea*	
Muscidae	Phaoniinae	Phaoniini	*Sinophaonia*	
Muscidae	Phaoniinae	Phaoniini	*Souzalopesmyia*	A4
Muscidae	Phaoniinae	Eginiini	*Eginia*	A8
Muscidae	Phaoniinae	Eginiini	*Neohelina*	
Muscidae	Phaoniinae	Eginiini	*Syngamoptera*	
Muscidae	Phaoniinae	Eginiini	*Xenotachina*	A8
Muscidae	Phaoniinae	Dichaetomyiini	*Aethiopomyia*	A4
Muscidae	Phaoniinae	Dichaetomyiini	*Alluaudinella*	A4
Muscidae	Phaoniinae	Dichaetomyiini	*Auria*	
Muscidae	Phaoniinae	Dichaetomyiini	*Dichaetomyia*	A4
Muscidae	Phaoniinae	Dichaetomyiini	*Ochromusca*	A4
Muscidae	Phaoniinae	Dichaetomyiini	*Tamilomyia*	
Muscidae	Mydaeinae		*Afromydaea*	A4
Muscidae	Mydaeinae		*Bryantina*	
Muscidae	Mydaeinae		*Chaetopapuaia*	
Muscidae	Mydaeinae		*Dimorphia*	A4
Muscidae	Mydaeinae		*Graphomya*	A4
Muscidae	Mydaeinae		*Gymnodia*	A4, A3
Muscidae	Mydaeinae		*Gymnopapuaia*	A0
Muscidae	Mydaeinae		*Hebecnema*	A4, A7
Muscidae	Mydaeinae		*Helinomydaea*	
Muscidae	Mydaeinae		*Hemichlora*	A8
Muscidae	Mydaeinae		*Lasiopelta*	A4
Muscidae	Mydaeinae		*Mydaea*	A6, A7, A8
Muscidae	Mydaeinae		*Myospila*	A4
Muscidae	Mydaeinae		*Opsolasia*	A4
Muscidae	Mydaeinae		*Papuaia*	

Table 1 (continued).

Family	Subfamily	Tribe	Genus	Character state(s)
Muscidae	Mydaeinae		*Papuaiella*	
Muscidae	Mydaeinae		*Pseudohelina*	A4
Muscidae	Mydaeinae		*Scenetes*	
Muscidae	Mydaeinae		*Scutellomusca*	A4
Muscidae	Mydaeinae		*Sinopelta*	
Muscidae	Coenosiinae	Limnophorini	*Agenamyia*	
Muscidae	Coenosiinae	Limnophorini	*Albertinella*	
Muscidae	Coenosiinae	Limnophorini	*Camptotarsopoda*	A4
Muscidae	Coenosiinae	Limnophorini	*Drepanocnemis*	
Muscidae	Coenosiinae	Limnophorini	*Exsul*	
Muscidae	Coenosiinae	Limnophorini	*Heliographa*	A4
Muscidae	Coenosiinae	Limnophorini	*Idiohelina*	
Muscidae	Coenosiinae	Limnophorini	*Limnohelina*	
Muscidae	Coenosiinae	Limnophorini	*Limnophora*	A4
Muscidae	Coenosiinae	Limnophorini	*Lispe*	A4
Muscidae	Coenosiinae	Limnophorini	*Lispoides*	A4
Muscidae	Coenosiinae	Limnophorini	*Neolimnophora*	A4
Muscidae	Coenosiinae	Limnophorini	*Ocypodomyia*	
Muscidae	Coenosiinae	Limnophorini	*Pachyceramyia*	A4
Muscidae	Coenosiinae	Limnophorini	*Paracoenosia*	
Muscidae	Coenosiinae	Limnophorini	*Paralimnophora*	
Muscidae	Coenosiinae	Limnophorini	*Rhabdotoptera*	
Muscidae	Coenosiinae	Limnophorini	*Spilogona*	A4, [A8]
Muscidae	Coenosiinae	Limnophorini	*Syllimnophora*	
Muscidae	Coenosiinae	Limnophorini	*Tapantiomyia*	A0
Muscidae	Coenosiinae	Limnophorini	*Tetramerinx*	
Muscidae	Coenosiinae	Limnophorini	*Thaumasiochaeta*	A5
Muscidae	Coenosiinae	Limnophorini	*Villeneuvia*	A4
Muscidae	Coenosiinae	Limnophorini	*Xenomyia*	
Muscidae	Coenosiinae	Coenosiini	*Altimyia*	
Muscidae	Coenosiinae	Coenosiini	*Amicitia*	
Muscidae	Coenosiinae	Coenosiini	*Anaphalantus*	A4
Muscidae	Coenosiinae	Coenosiini	*Andersonosia*	A4
Muscidae	Coenosiinae	Coenosiini	*Apsil*	A4
Muscidae	Coenosiinae	Coenosiini	*Aztecamyia*	
Muscidae	Coenosiinae	Coenosiini	*Bithoracochaeta*	A4
Muscidae	Coenosiinae	Coenosiini	*Brevicosta*	A4
Muscidae	Coenosiinae	Coenosiini	*Cephalispa*	A4
Muscidae	Coenosiinae	Coenosiini	*Coenosia*	A4, [A7]
Muscidae	Coenosiinae	Coenosiini	*Cordiluroides*	A7
Muscidae	Coenosiinae	Coenosiini	*Insulamyia*	

Table 1 (continued).

Family	Subfamily	Tribe	Genus	Character state(s)
Muscidae	Coenosiinae	Coenosiini	*Limnospila*	A4
Muscidae	Coenosiinae	Coenosiini	*Lispocephala*	A4
Muscidae	Coenosiinae	Coenosiini	*Macrorchis*	A4
Muscidae	Coenosiinae	Coenosiini	*Microcalyptra*	
Muscidae	Coenosiinae	Coenosiini	*Neodexiopsis*	A4
Muscidae	Coenosiinae	Coenosiini	*Notoschoenomyza*	A4
Muscidae	Coenosiinae	Coenosiini	*Orchisia*	A4
Muscidae	Coenosiinae	Coenosiini	*Oxytonocera*	A4
Muscidae	Coenosiinae	Coenosiini	*Palpilongus*	
Muscidae	Coenosiinae	Coenosiini	*Parvisquama*	A4
Muscidae	Coenosiinae	Coenosiini	*Pentacricia*	
Muscidae	Coenosiinae	Coenosiini	*Pilispina*	
Muscidae	Coenosiinae	Coenosiini	*Plumispina*	
Muscidae	Coenosiinae	Coenosiini	*Pseudocoenosia*	A4
Muscidae	Coenosiinae	Coenosiini	*Pygophora*	A4
Muscidae	Coenosiinae	Coenosiini	*Reynoldsia*	A4
Muscidae	Coenosiinae	Coenosiini	*Schoenomyza*	A4
Muscidae	Coenosiinae	Coenosiini	*Schoenomyzina*	A4
Muscidae	Coenosiinae	Coenosiini	*Spanochaeta*	A4
Muscidae	Coenosiinae	Coenosiini	*Spathipheromyia*	A4
Muscidae	Coenosiinae	Coenosiini	*Stomopogon*	A4
Muscidae	Coenosiinae	Coenosiini	*Sumapazomyia*	

- *Australofannia* Pont, 1977 (Figs 3A–D, 4A–B)

This genus consists of *Australofannia spiniclunis* Pont, 1977 and one undescribed species, both endemic to Australia (Pont 1977). Examination of *A. spiniclunis* revealed a costal chaetotaxy deviating substantially from the usual fanniid pattern. Both sexes (Figs 3–4) have vein C extensively setulose both ventrally and dorsally (state **A8**). Further, extensive weakening of the costal spinules has taken place: the lower anterior costal row is wholly setulose in both sexes, whereas the upper anterior row has retained the usual spinule-setula pattern in the female (Figs 3A–C, 4A), but with only a few spinules distally on CS1 in the male sex (Fig. 4B).

Family **Muscidae** Latreille, 1802

The Muscidae with ca 5000 described species represent one of the largest radiations among the calyptrate families. The classification adopted here is fairly conventional, morphology based, but slightly updated according to results obtained from analyses of molecular data presented in particular by Kutty *et al.* (2014). It recognizes eight subfamilies, seven tribes and 179 genus-group taxa (Table 1).

Species from 115 muscid genera and subgenera have presently been examined for the distribution of setulae ventrally and dorsally on vein C (character **A**) in agreement with the nine states described above (Table 1).

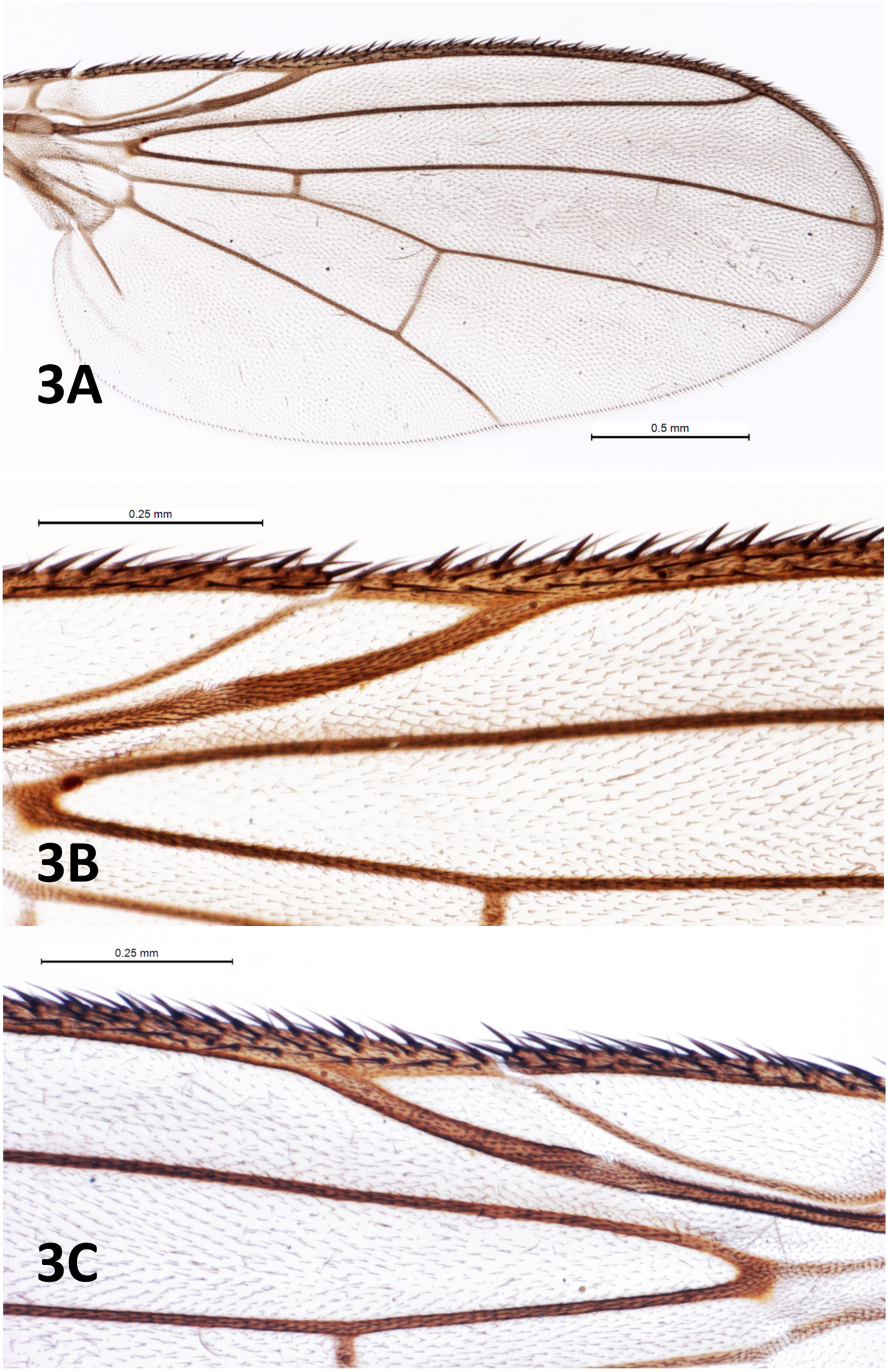

Fig. 3. *Australofannia spiniclunis* Pont, 1977, ♀. **A**. Wing, ventral view. **B**. Detail of wing showing CS1–3, ventral view. **C**. Detail of wing showing CS1–3, dorsal view.

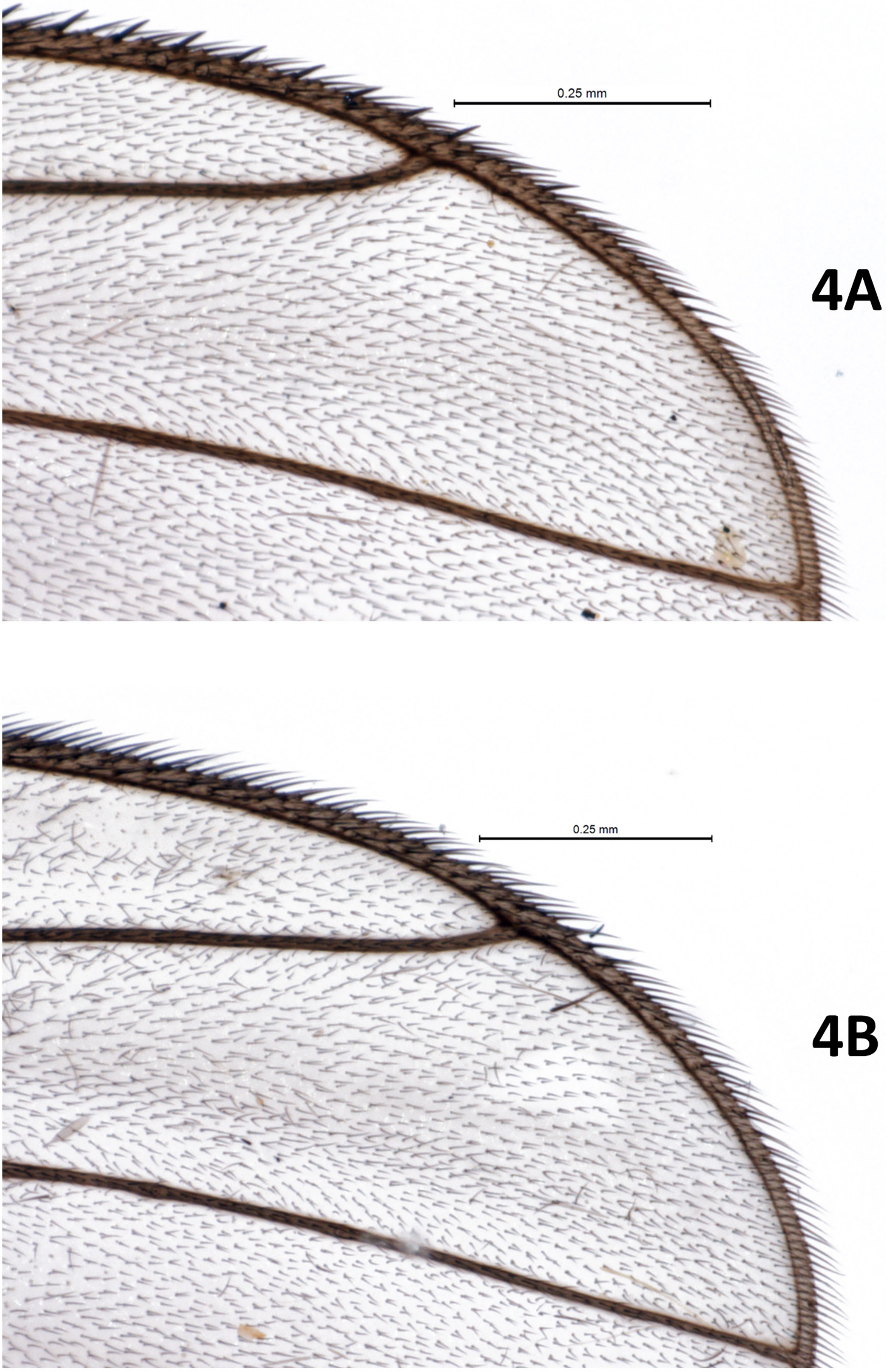

Fig. 4. *Australofannia spiniclunis* Pont, 1977, detail of wing showing CS3–4, dorsal view. **A**. ♀. **B**. ♂.

Subfamily **Azeliinae** Robineau-Desvoidy, 1830

A subfamily of 'lower' Muscidae including the former Achanthipterinae Hennig, 1962 (Kutty *et al.* 2014). Species from nine of a total of 12 recognized genera were examined (Table 1).

- *Achanthiptera* Rondani, 1856

The only known species, *Achanthiptera rohrelliformis* (Robineau-Desvoidy, 1830), has vein C extensively setulose ventrally and bare dorsally (state **A4**).

- *Potamia* Robineau-Desvoidy, 1830

Both examined species, *Potamia littoralis* Robineau-Desvoidy, 1830 and *P. setifemur* (Stein, 1916), have vein C extensively setulose ventrally and bare dorsally (state **A4**).

- *Australophyra* Malloch, 1923

The only known species, *Australophyra rostrata* (Robineau-Desvoidy, 1830), has the ventral costal setulae confined to CS1 (state **A2)**.

- *Azelia* Robineau-Desvoidy, 1830 (Fig. 5A–B)

A total of 10 species was examined. They all have vein C bare ventrally (state **A0**), as shown by *Azelia cilipes* (Haliday, 1838) (Fig. 5A–B).

- *Drymeia* Meigen, 1826 (Fig. 6A–C)

A large, morphologically varied genus found primarily in the northern and elevated parts of the Holarctic region. More than 10 examined species of *Drymeia*, including some unidentified ones, agree with *Azelia* in the absence of ventral costal setulae (state **A0**), as shown by *D. vicana* (Harris, 1780) (Fig. 6A). One species, *D. hamata* (Fallén, 1823) (Fig. 6B–C), differs by having vein C extensively setulose ventrally (state **A4**).

Ventral setulae are also seen on CS1 in *Drymeia tetra* (Meigen, 1826) and some *D. alpicola* (Rondani, 1871), but these are setulae displaced from the lower anterior spinule-setula row.

- *Hydrotaea* Robineau-Desvoidy, 1830 (Fig. 7A–C)

Examination of a large number of species showed that vein C is bare dorsally and with a trend towards loss of ventral costal setulae.

Two species, *Hydrotaea cyrtoneurina* (Zetterstedt, 1845) (Fig. 7A) and *H. ringdahli* Stein, 1916, have vein C extensively setulose ventrally (state **A4**).

The following species have ventral costal setulae confined to CS1 (state **A2**): *Hydrotaea anxia* (Zetterstedt, 1838), *H. cyaneiventris* Macquart, 1851, *H. dentipes* (Fabricius, 1805) (Fig. 7B), *H. hirticeps* (Fallén, 1824), *H. militaris* (Meigen, 1826), *H. palaestrica* (Meigen, 1826) and *H. similis* Meade, 1887.

Some species have ventral setulae on less than the basal half of CS1 (state **A1**): *Hydrotaea capensis* (Wiedemann, 1818), *H. chalcogaster* (Wiedemann, 1824), *H. diabolus* (Harris, 1780) and *H. ignava* (Harris, 1780).

Most species examined are without ventral setae on vein C (state **A0**): *Hydrotaea aenescens* (Wiedemann, 1830), *H. borussica* Stein, 1899, *H. cinerea* Robineau-Desvoidy, 1830, *H. floccosa* Macquart, 1835, *H. irritans* (Fallén, 1823), *H. glabricula* (Fallén, 1825), *H. meridionalis* Portschinsky, 1882, *H. meteorica* (Linnaeus, 1758) (Fig. 7C), *H. pandellei* Stein, 1899, *H. pellucens* Portschinsky, 1879, *H. penicillata*

(Rondani, 1866), *H. pilipes* Stein, 1903, *H. pilitibia* Stein, 1916, *H. scambus* (Zetterstedt, 1838), *H. tuberculata* Rondani, 1866 and *H. unispinosa* Stein, 1898.

In *Hydrotaea borussica*, *H. irritans* and allied species, the lower anterior spinule-setula row on the basal part of CS1 consists of setulae only, some of which are frequently displaced ventrally.

- *Neohydrotaea* Malloch, 1924

The only examined species, *Neohydrotaea lundbecki* (Michelsen, 1978), has vein C bare dorsally and extensively setulose ventrally (state **A4**).

- *Thricops* Rondani, 1856

Examination of a large number of species revealed that most of them have vein C bare dorsally and extensively setulose ventrally (state **A4**): *Thricops aculeipes* (Zetterstedt, 1838), *T. beckeri* (Pokorny, 1893), *T. culminum* (Pokorny, 1889), *T. cunctans* (Meigen, 1826), *T. foveolatus* (Zetterstedt, 1845), *T. furcatus* (Stein, 1916), *T. genarum* (Zetterstedt, 1838), *T. hirtulus* (Zetterstedt, 1838), *T. innocuus*

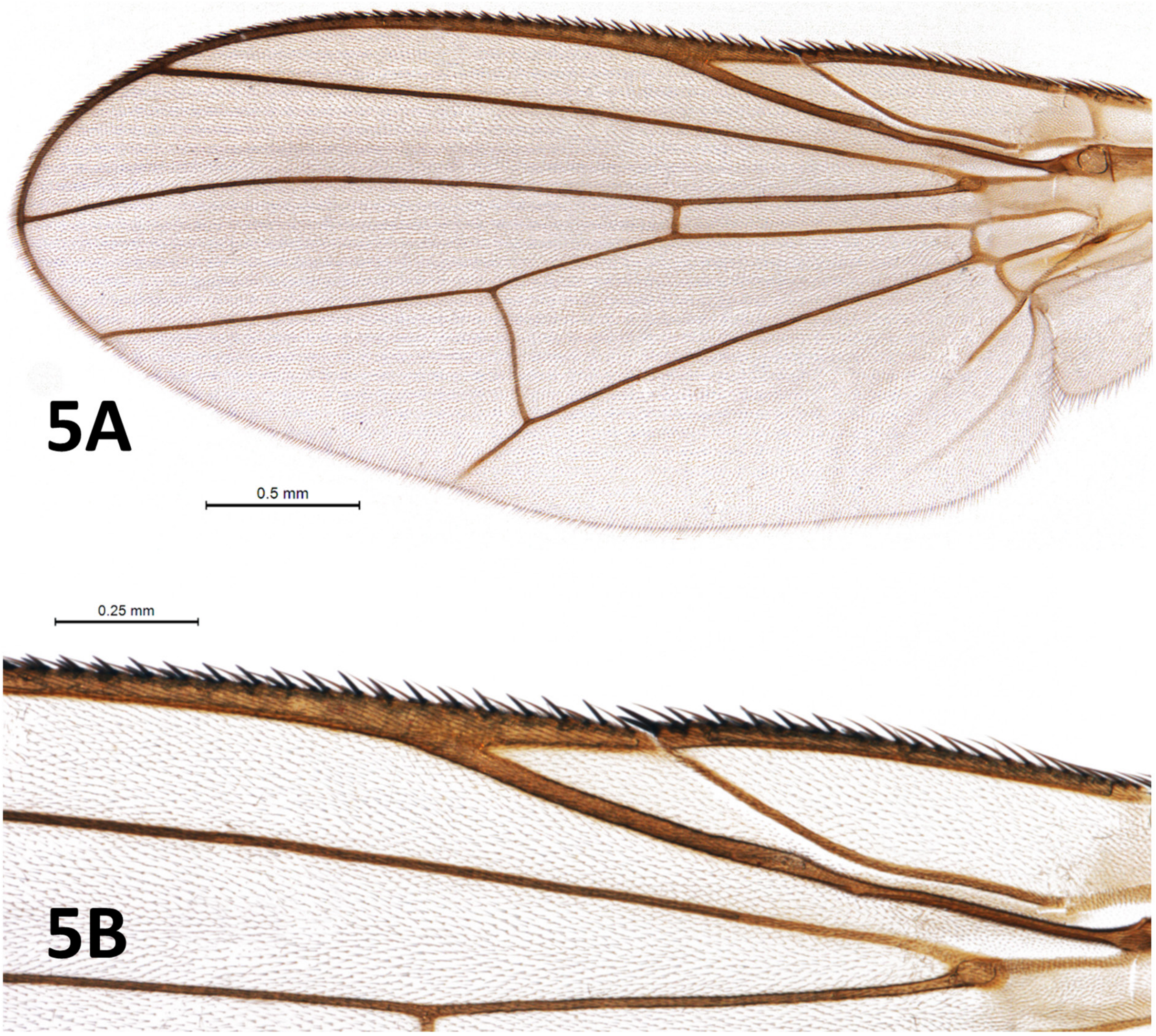

Fig. 5. *Azelia cilipes* (Haliday, 1838) ♀. **A**. Wing, ventral view. **B**. Detail of wing showing CS1–3, ventral view.

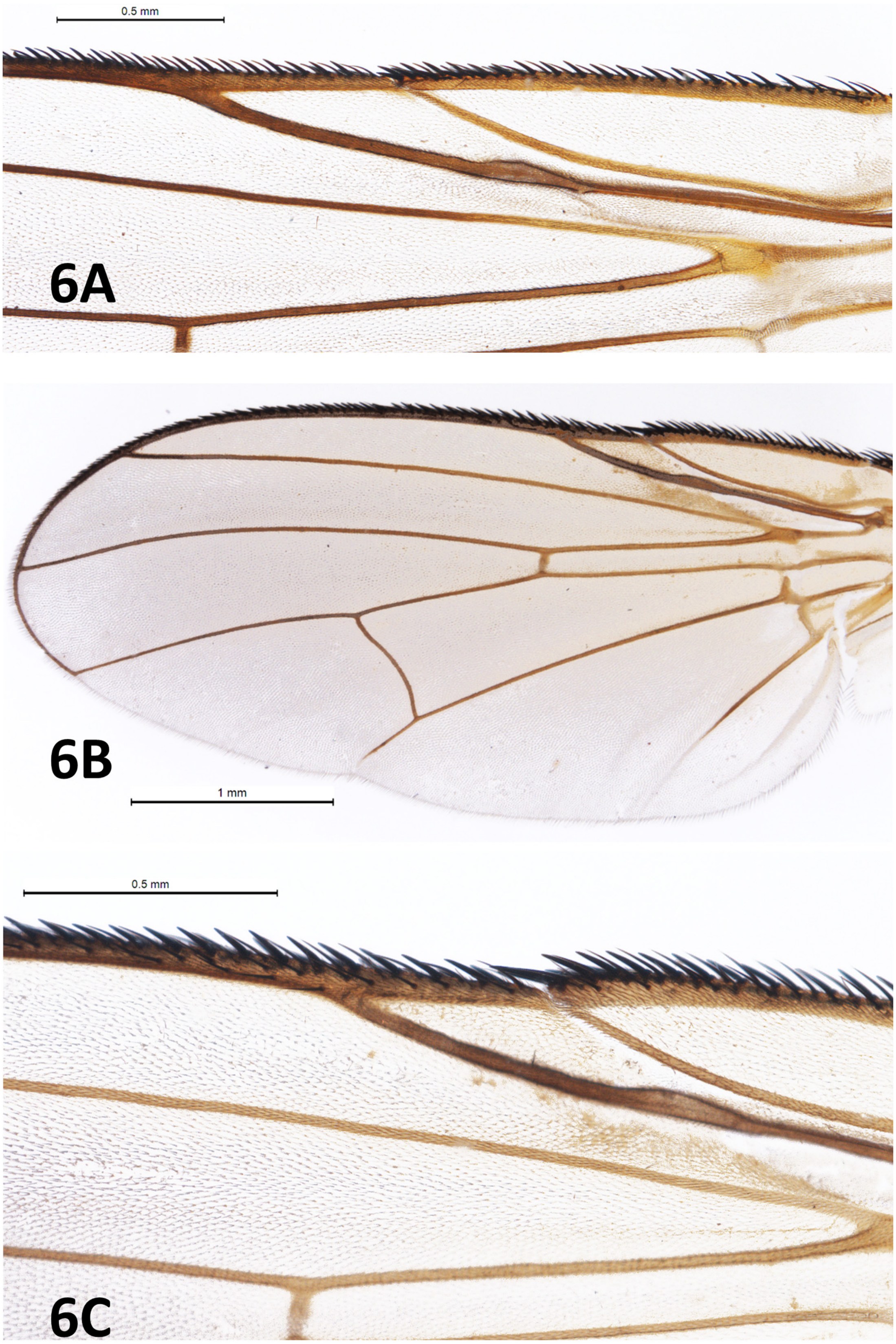

Fig. 6. ♀♀ of *Drymeia* Meigen, 1826. **A**. *D. vicana* (Harris, 1780), detail of wing showing CS1–3, ventral view. **B**. *D. hamata* (Fallén, 1823), wing, ventral view. **C**. Same, detail of wing showing CS1–3, ventral view.

(Zetterstedt, 1838), *T. longipes* (Zetterstedt, 1845), *T. nigrifrons* (Robineau-Desvoidy, 1830), *T. nigritellus* (Zetterstedt, 1838), *T. rostratus* (Meade, 1882), *T. semicinereus* (Wiedemann, 1817), *T. separ* (Zetterstedt, 1845), *T. septentrionalis* (Stein, 1898), *T. simplex* (Wiedemann, 1817) (males), *T. spiniger* (Stein, 1904), *T. sudeticus* (Schnabl, 1888), *T. tomkovichi* Vikhrev in Vikhrev & Sorokina, 2009 and *T. vaderi* Savage, 2003.

Females of *Thricops simplex* tend to have a short, irregular row of dorsal costal setulae on CS2 and adjacent basal part of CS3 (state **A6**).

A more extensive row of dorsal costal setulae on CS2 and CS3 (state **A7**) is seen in *Thricops albibasalis* (Zetterstedt, 1849), *T. lividiventris* (Zetterstedt, 1845) and *T. rufisquamus* (Schnabl, 1915) (only female examined).

In *Thricops diaphanus* (Wiedemann, 1817), the dorsal costal setulae tend to occupy CS1–3 (state **A8**), although bare patches distally on CS1 and on CS2 do occur in some males.

- *Huckettomyia* Pont & Shinonaga, 1970

A small, exclusively northern Palaeartic genus. The single male of *Huckettomyia watanabei* Pont & Shinonaga, 1970 examined is extensively setulose on the dorsal side of vein C (state **A8**).

Subfamily **Muscinae** Latreille, 1802

In this large, but well-defined and conceivably monophyletic subfamily, vein C is always bare dorsally, while the development of ventral setulae varies substantially among and within the genera.

Tribe **Muscini** Latreille, 1802

This tribe is now suspected of being paraphyletic, because molecular studies (Kutty *et al*. 2014, 2019) nest Stomoxyini within the Muscini as presently understood. Grzywacz *et al.* (2021), based on molecular approaches, even suggested a classification in which the traditional Muscini genera *Mesembrina* and *Polietes* are moved to the Azeliinae. This classification is not adopted here in the absence of morphological support. Species from 17 of 23 currently recognized genera and subgenera (Table 1) have been examined, but data from the remaining genus-group taxa (names marked with an asterisk below) have been extracted from Nihei & de Carvalho (2007), who performed a character analysis of the Muscini that involved scoring of the presence/absence of setulae ventrally on CS1 or CS1–CS3.

- *Biopyrellia* Townsend, 1932, *Curranosia* Paterson, 1957, *Dasyphora* Robineau-Desvoidy, 1830 (including subgenera *Eudasyphora* Townsend, 1911 and *Rypellia* Malloch, 1931), *Deltotus* Séguy, 1935*, *Hennigmyia* Peris, 1967, *Mitroplatia* Enderlein, 1935, *Morellia* Robineau-Desvoidy, 1830 (including subgenera *Parapyrellia* Townsend, 1915, *Trichomorellia* Stein, 1918* and *Xenomorellia* Malloch, 1923*), *Myiophaea* Enderlein, 1935, *Neorypellia* Pont, 1972*, *Polietina* Schnabl & Dziedzicki, 1911*, *Pyrellina* Malloch, 1923, *Sarcopromusca* Townsend, 1927* and *Ziminellia* Nihei & de Carvalho, 2007

The examined species belonging to these genera/subgenera of Muscini share the prevalent muscid state **A4** in which vein C is bare dorsally and extensively setulose ventrally: *Biopyrellia bipuncta* (Wiedemann, 1830), *Curranosia gemma* (Bigot, 1878), *Dasyphora* (*Dasyphora*) (6 spp), *D.* (*Eudasyphora*) (4 spp), *D.* (*Rypellia*) (3 spp), *Hennigmyia setinervis* (Stein, 1913), *Mitroplatia* (4 spp), *Morellia* (*Morellia*) (12 spp), *M.* (*Parapyrellia*) (1 sp.), *Myiophaea spissa* (Walker, 1858), *Pyrellina* (3 spp) and *Ziminellia* (3 spp). The other genera and subgenera in the list above that are tagged with an asterisk were scored for character **A** by Nihei & de Carvalho (2007).

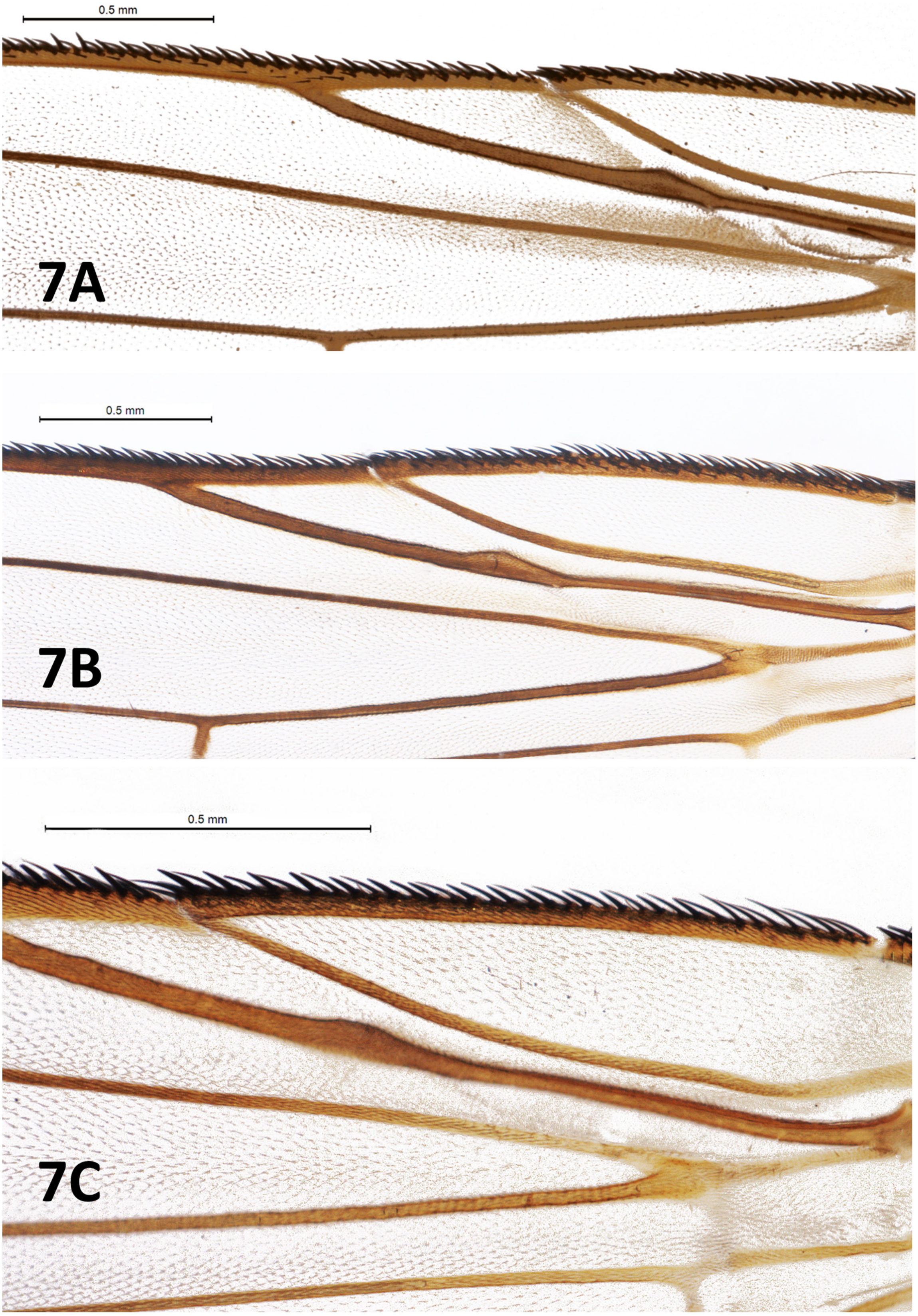

Fig. 7. ♀♀ of *Hydrotaea* Robineau-Desvoidy. **A**. *H. cyrtoneurina* (Zetterstedt, 1845), detail of wing showing CS1–3, ventral view. **B**. *H. dentipes* (Fabricius, 1805), detail of wing showing CS1–3, ventral view. **C**. *H. meteorica* (Linnaeus, 1758), detail of wing showing CS1–2, ventral view.

- *Mesembrina* Meigen, 1826

A small, distinctive genus of large and robust Muscidae. Nihei & de Carvalho (2007) observed that species of *Mesembrina* have the ventral setulae on vein C confined to CS1 (state **A2**). My examination of the following species confirms this: *M. latreillii* Robineau-Desvoidy, 1830, *M. meridiana* (Linnaeus, 1758), *M. mystacea* (Linnaeus, 1758) and *M. resplendens* Wahlberg, 1844.

- *Musca* Linnaeus, 1758 (Fig. 8A–C)

As pointed out by Nihei & de Carvalho (2007), the distribution of ventral costal setulae varies among species of the large cosmopolitan genus *Musca*. Character **A** as presently defined divides the 37 examined species into three groups:

Most species have the entire CS1occupied by ventral setulae (state **A2**): *Musca aethiops* Stein, 1913, *M. alpesa* Walker, 1849, *M. autumnalis* De Geer, 1776, *M. bakeri* Patton, 1923, *M. bezzii* Patton & Cragg, 1913, *M. convexifrons* Thomson, 1869, *M. craggy* Patton, 1922 (female only), *M. domestica* Linnaeus, 1758 (Fig. 8A), *M. formosana* Malloch, 1925, *M. gabonensis* Macquart, 1855, *M. inferior* Stein, 1909, *M. larvipara* Portschinsky, 1910, *M. liberia* Snyder, 1951, *M. lindneri* Paterson, 1956, *M. lusoria* Wiedemann, 1824, *M. pattoni* Austen, 1910, *M. planiceps* Wiedemann, 1824, *M. seniorwhitei* Patton, 1922, *M. ventrosa* Wiedemann, 1830 and *M. xanthomelaena* Wiedemann, 1824.

Several species have the ventral costal setae occupying the basal quarter to basal half of CS1 (state **A1**): *Musca afra* Paterson, 1956, *M. albina* Wiedemann, 1830, *M. biseta* Hough, 1898, *M. cassara* Pont, 1973, *M. conducens* Walker, 1859, *M. confiscata* Speiser, 1924, *M. craggy* (male only), *M. crassirostris* Stein in Becker, 1903, *M. dasyops* Stein, 1913, *M. lasiophthalma* Thomson, 1869, *M. munroi* Patton, 1936, *M. sorbens* Wiedemann, 1830 (Fig. 8B), *M. tempestiva* Fallén, 1817 and *M. vetustissima* Walker, 1849.

A few species are without ventral costal setulae or have at most a few setulae at the extreme base of CS1 (state **A0**): *Musca lucidula* Loew, 1856, *M. osiris* Wiedemann, 1830 and *M. vitripennis* Meigen, 1826 (Fig. 8C).

- *Neomyia* Walker, 1859 (Fig. 9A–B)

As noticed by Nihei & de Carvalho (2007), the large cosmopolitan genus *Neomyia* varies with respect to the distribution of ventral costal setulae. Character **A** divides the 31 species presently examined in two groups as follows:

One group has vein C extensively setulose ventrally, which is the prevailing muscid state **A4**: *Neomyia aureopyga* (Malloch, 1923), *N. australis* (Macquart, 1848), *N. claripennis* (Malloch, 1923), *N. currani* (Pont in Crosskey, 1980)*, N. diffidens* (Walker, 1856), *N. intacta* (Curran, 1935), *N. laxifrons* (Villeneuve, 1916), *N. limbata* (Villeneuve, 1916), *N. marginipennis* (Stein, 1918), *N. nudissima* (Loew, 1852) (Fig. 9A), *N. rubrifacies* (Malloch, 1923) and *N. zumpti* (Zielke, 1971).

The other, larger group of species has the ventral costal setulae confined to CS1 (state **A2**): *Neomyia albigena* (Stein, 1913), *N. chrysopyga* (Emden, 1939), *N. coeruleifrons* (Macquartt, 1851), *N. cornicina* (Fabricius, 1781) (Fig. 9B), *N. dubia* (Malloch, 1923), *N. fletcheri* (Emden & Aubertin in Emden, 1965), *N. gavisa* (Walker, 1859), *N. indica* (Robineau-Desvoidy, 1830), *N. laevifrons* (Loew, 1858), *N. lauta* (Wiedemann, 1830), *N. peronii* (Robineau-Desvoidy, 1830), *N. racilia* (Walker, 1859), *N. rhingiaeformis* (Villeneuve, 1914), *N. sororella* (Villeneuve, 1926), *N. sperata* (Walker, 1859), *N. splendida* (Adams, 1905), *N. timorensis* (Robineau-Desvoidy, 1830), *N. viridescens* (Robineau-Desvoidy, 1830) and *N. viridifrons* (Macquart, 1843).

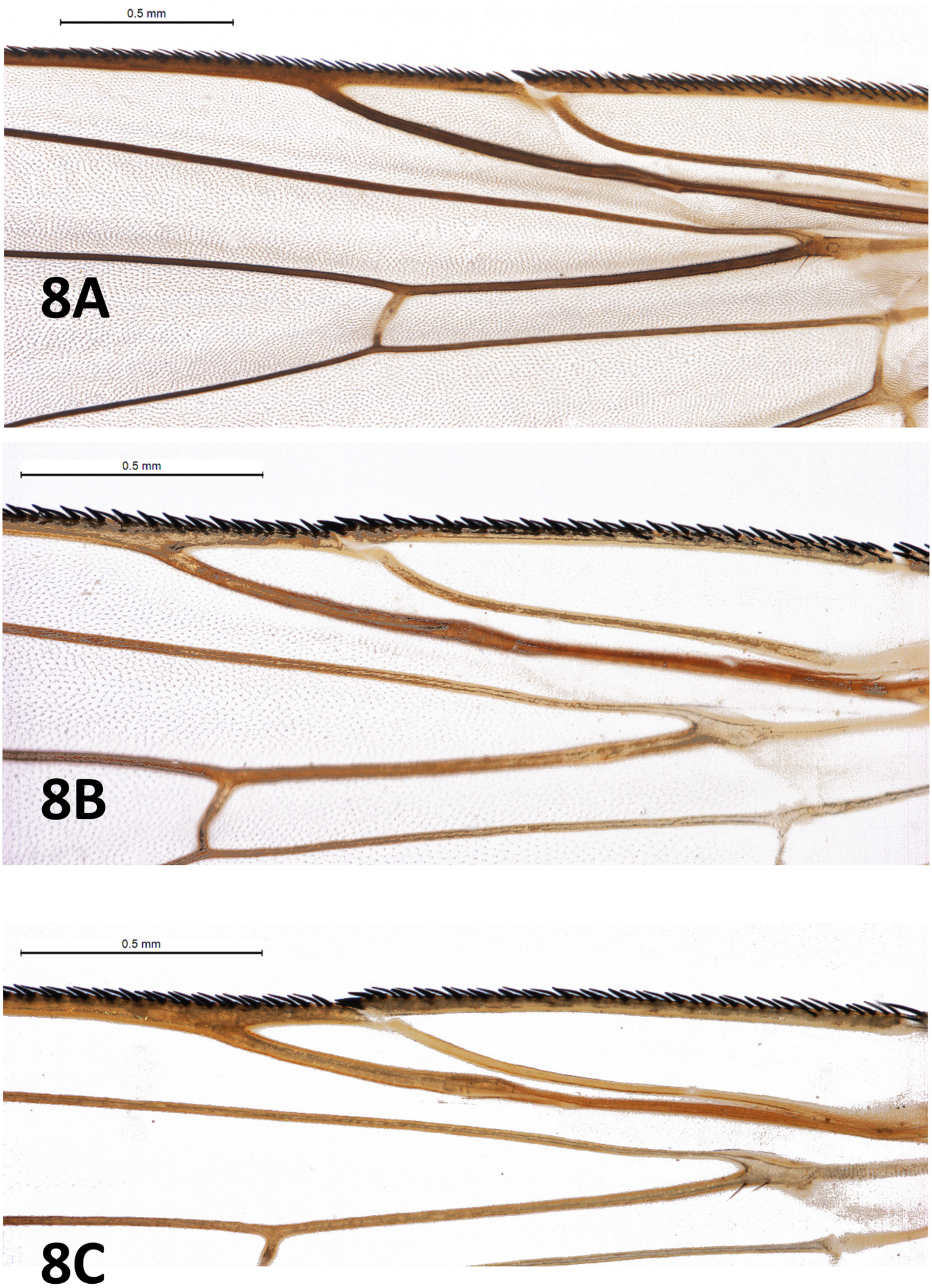

Fig. 8. ♀♀ of *Musca* Linnaeus, 1758. **A**. *M. domestica* Linnaeus, 1758, detail of wing showing CS1–3, ventral view. **B**. *M. sorbens* Wiedemann, 1830, detail of wing showing CS1–3, ventral view. **C**. *M. vitripennis* Meigen, 1826, detail of wing showing CS1–3, ventral view.

- *Polietes* Rondani, 1866 (Fig. 10A–C)

As noticed by Nihei & de Carvalho (2007), differences in the distribution of ventral costal setulae divide the small genus *Polietes* in the same way as seen in *Neomyia*:

Three medium-sized species examined have vein C extensively setulose ventrally (state **A4**): *Polietes domitor* (Harris, 1780) (Fig. 10A–B), *P. major* (Ringdahl, 1926) and *P. steinii* (Ringdahl, 1913).

Three large species examined have the ventral costal setulae confined to CS1 (state **A2**): *Polietes lardarius* (Fabricius, 1781) (Fig. 10C), *P. meridionalis* Peris & Llorente, 1963 and *P. nigrolimbatus* (Bonsdorff, 1866).

- *Pyrellia* Robineau-Desvoidy, 1830

A difference in the distribution of ventral costal setulae determined by gender rather than species was observed in the five species presently examined: *Pyrellia albocuprea* Villeneuve, 1914, *P. rapax* (Harris,

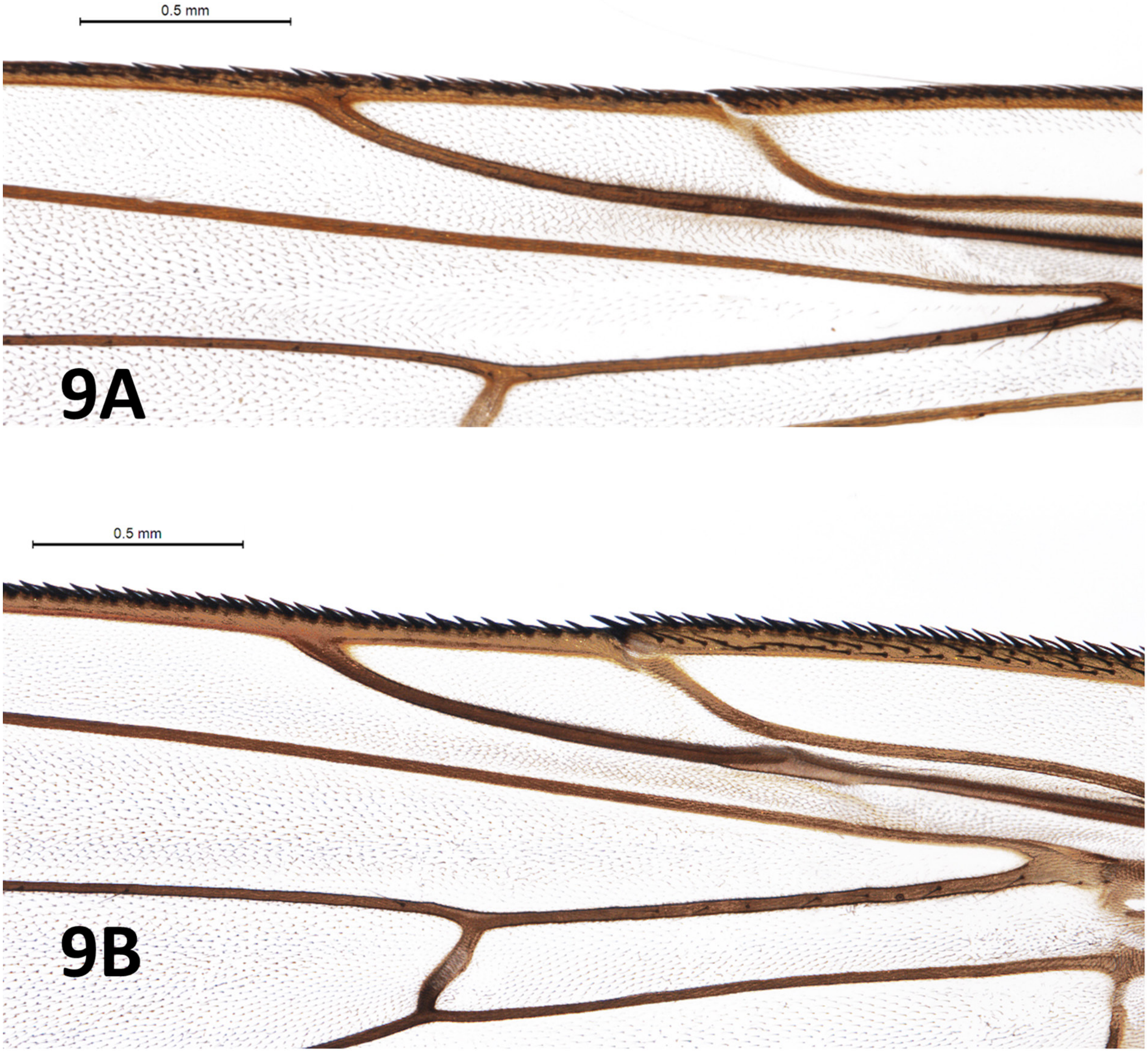

Fig. 9. ♀♀ of *Neomyia* Walker, 1859. **A**. *N. nudissima* (Loew, 1852), detail of wing showing CS1–3, ventral view. **B**. *N. cornicina* (Fabricius, 1781), detail of wing showing CS1–3, ventral view.

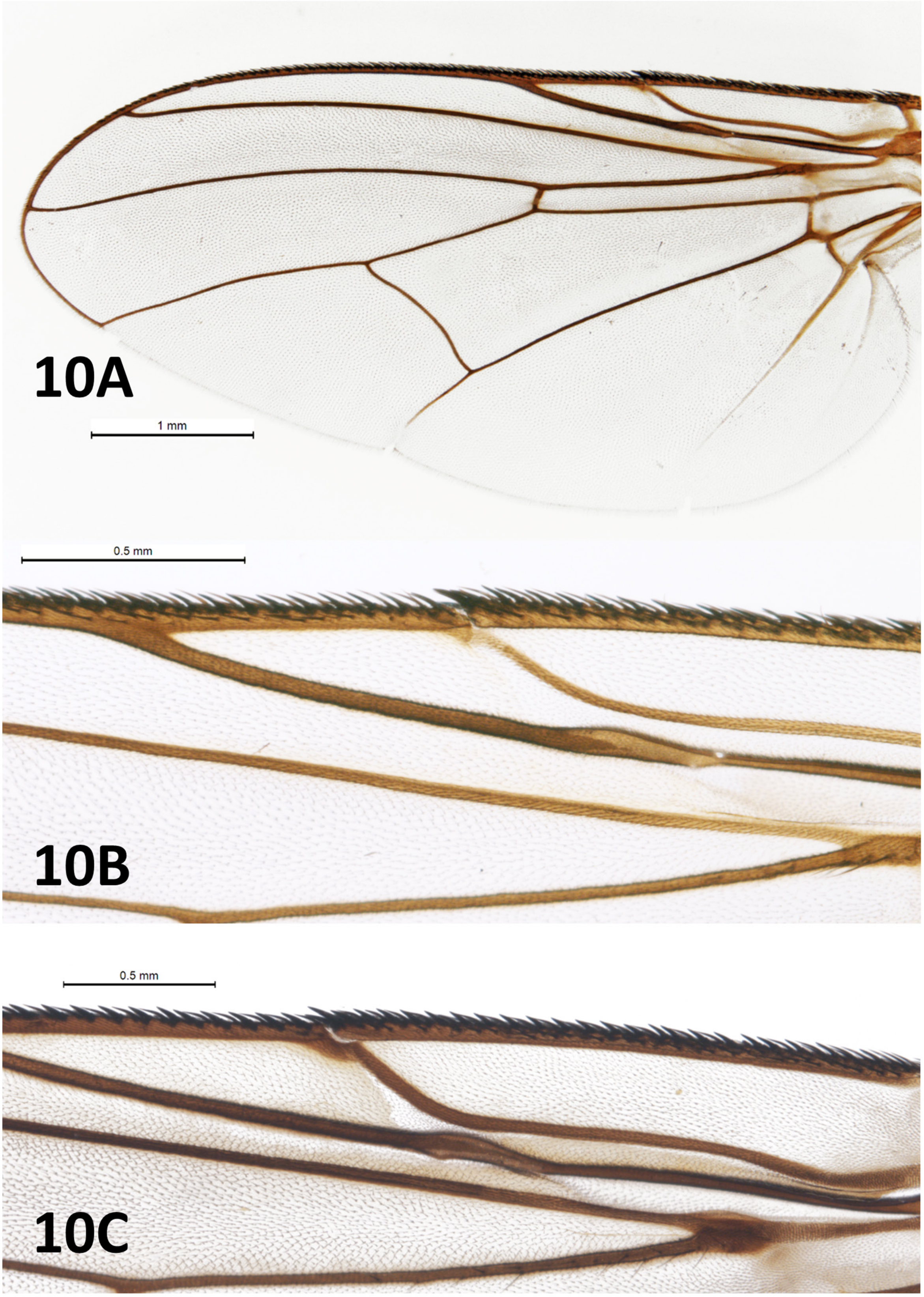

Fig. 10. ♀♀ of *Polietes* Rondani, 1866. **A**. *P*. *domitor* (Harris, 1780), wing, ventral view. **B**. Same, detail of wing showing CS1–2, ventral view. **C**. *P*. *lardarius* (Fabricius, 1781), detail of wing showing CS1–2, ventral view.

1780), *P. scintillans* Bigot, 1888, *P. tasmaniae* Macquart, 1846 and *P. vivida* Robineau-Desvoidy, 1830. The females have ventral setulae all over CS1 (state **A2**), while these setulae only occupy the basal half or less of CS1 (state **A1**) in the males.

Tribe **Stomoxyini** Meigen, 1824

The specialized mouthparts of this group of hematophagous muscids leave no doubt as to their monophyly. Among the 10 currently recognized genera I have examined species belonging to five of them (Table 1).

- *Haematobia* Le Peletier & Serville in Latreille *et al.*, 1828

The examined species *Haematobia exigua* Meijere in Schat, 1903, *H. irritans* (Linnaeus, 1758) and *H. minuta* (Bezzi, 1892), have vein C extensively setulose ventrally (state **A4**), but one examined species or subspecies (*Haematobia thirouxi titillans* (Bezzi, 1907)) has the ventral costal setulae confined to CS1 (state **A2**).

- *Haematobosca* Bezzi, 1907

Among the five examined species, *Haematobosca alcis* (Snow, 1891) and *H. sanguisugens* (Austen, 1909), stat. rev., have vein C extensively setulose ventrally (state **A4**), *H. sanguinolenta* (Austen, 1909) and *H. stimulans* (Meigen, 1824) have the ventral costal setulae confined to CS1 (state **A2**), and *Haematobosca atripalpis* (Bezzi, 1895) has the ventral setulae confined to the basal half of CS1 (state **A1**).

- *Neivamyia* Pinto & Fonseca, 1930

The only examined species, *Neivamyia flavicornis* (Malloch, 1928), has the ventral costal setulae confined to CS1 (state **A2**).

- *Stomoxys* Geoffroy, 1762

In most examined species (*Stomoxys calcitrans* (Linnaeus, 1758), *S. inornatus* Grünberg, 1906, *S. niger* Macquart, 1851, *S. pallidus* Roubaud, 1911, *S. sitiens* Rondani, 1873 and *S. taeniatus* Bigot, 1888) vein C is extensively setulose ventrally (state **A4**), but in one species (*Stomoxys indicus* Picard, 1908) the ventral costal setulae are confined to CS1 (state **A2**).

- *Stygeromyia* Austen, 1907

In the only examined species, *Stygeromyia sanguinaria* Austen, 1909, vein C is bare ventrally except for single setulae at the extreme base of CS1 (state **A0**).

Subfamily **Atherigoninae** Fan, 1965

This subfamily includes only one large genus of morphologically deviant Muscidae. It is obviously monophyletic, but its relationships remain uncertain.

- *Atherigona* Rondani, 1856 (Fig. 11A–B)

A total of 20+ named and unidentified species of *Atherigona* from the Old World tropics and Mediterranean subregion were examined. They invariably share state **A0**, in which vein C is wholly bare ventrally behind the lower anterior row of alternating spinules and setulae, as exemplified by *A. orientalis* Schiner, 1868 (Fig. 11A–B).

Subfamily **Reinwardtiinae** Brauer & Bergenstamm, 1889

This taxon is a heterogeneous, para- or polyphyletic assemblage of genera which is also reflected in its diverse costal chaetotaxy. Species from seven among the 15 currently recognized genera (Table 1) were examined.

- *Muscina* Robineau-Desvoidy, 1830 (Fig. 12A), *Passeromyia* Rodhain & Villeneuve, 1915, *Philornis* Meinert, 1890

The examined species belonging to the above genera of Reinwardtiinae share the prevalent muscid state **A4** in which vein C is bare dorsally and extensively setulose ventrally: *Muscina* (5 spp), *Passeromyia heterochaeta* Villeneuve, 1915 and *P. steini* Pont, 1970, *Philornis* (5 spp).

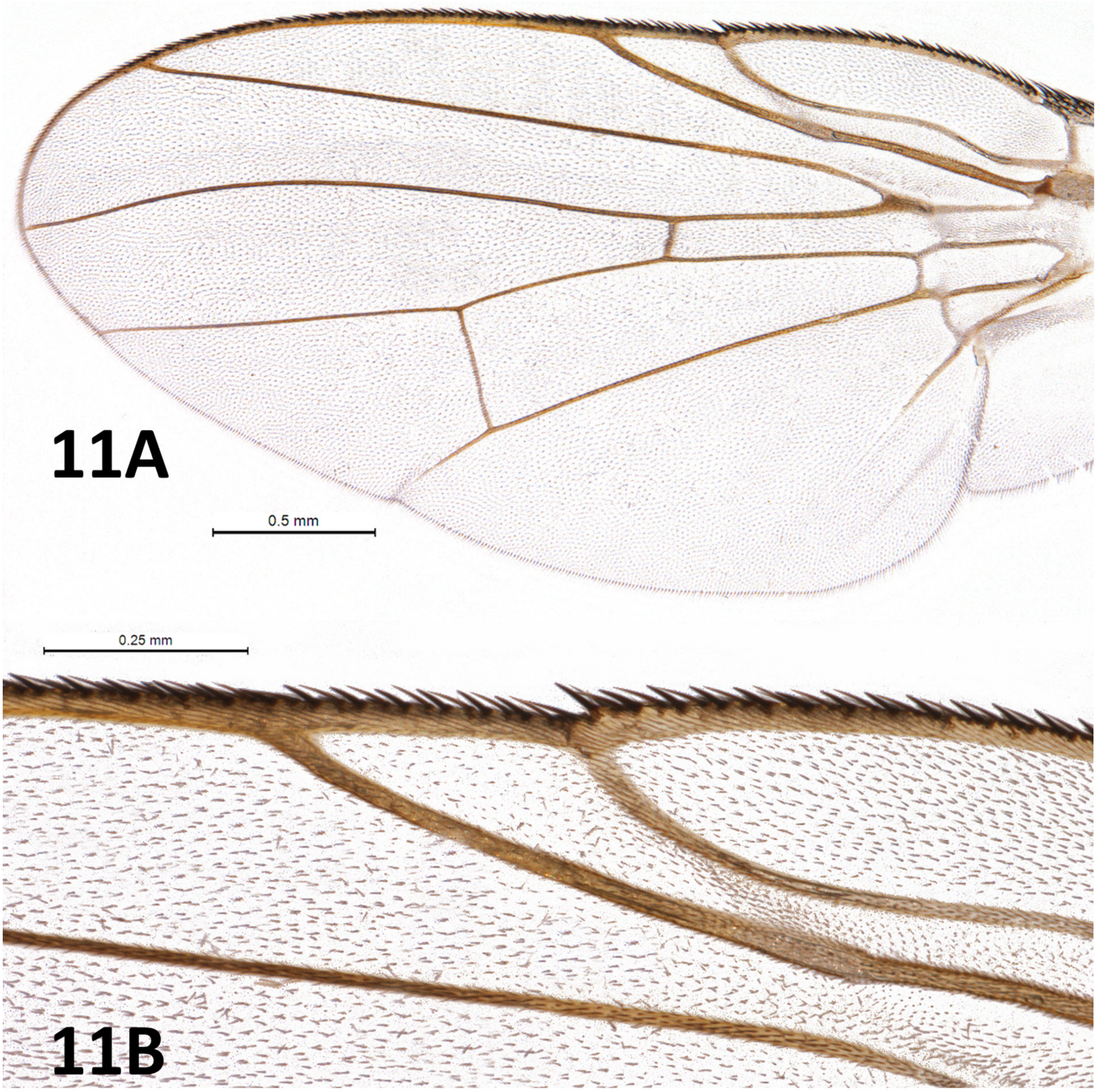

Fig. 11. *Atherigona orientalis* Schiner, 1868, ♀. **A**. Wing, ventral view. **B**. Detail of wing showing CS1–3, ventral view.

- *Synthesiomyia* Brauer & Bergenstamm, 1893

The only included species, *Synthesiomyia nudipes*, has vein C only fully setulose ventrally on CS2 (state **A2**), although some irregular ventral costal setulae extent onto CS2 or (females only) even the basal part of CS3.

- *Brachygasterina* Macquart, 1851, *Palpibracus* Rondani, 1863 (Fig. 12B), *Psilochaeta* Stein, 1911

The examined species of these three exclusively South American genera differ substantially from the preceding reinwardtiine genera by the dorsally extensively setulose vein C (state **A8**, Fig. 12B): *Brachygasterina fulvohumeralis* (Malloch, 1922), *B. violaceiventris* Macquart, 1851, *Palpibracus* (12 spp) and *Psilochaeta chalybea* (Wiedemann, 1830). Only *Brachygasterina major* Malloch, 1934 differs by having the dorsal setulae restricted to CS2 and CS3 (females) or CS3 (males) (state **A7**).

Subfamily **Cyrtoneurininae** Snyder, 1954

This is essentially a Neotropical group extending into southern North America. It is rather heterogeneous and doubtfully monophyletic. Among the currently included 12 genera I have examined species from five of them (Table 1). They all agree in having vein C extensively setulose ventrally.

- *Cyrtoneurina* Giglio-Tos, 1893, *Cyrtoneuropsis* Malloch, 1925, *Neomuscina* Townsend, 1919

The examined species of the above genera share the prevalent muscid state **A4** in which vein C is bare dorsally and extensively setulose ventrally: *Cyrtoneurina* (2 spp indet.), *Cyrtoneuropsis* (8 spp), *Neomuscina rufoscutella* Dodge, 1955 and *N. tripunctata* Wulp, 1896.

- *Arthurella* Albuquerque, 1954

Among the two species examined, *Arthurella nudiseta* Albuquerque, 1954 has vein C extensively setulose dorsally (state **A8**), while *A. choelensis* Patitucci & Mariluis in Patitucci *et al.*, 2011 is without dorsal setulae on CS1 (state **A7**).

- *Pseudoptilolepis* Snyder, 1949

The only examined species, *P. confusa* Snyder, 1949, has vein C extensively setulose dorsally (state **A8**).

Subfamily **Phaeoniinae** Malloch, 1917

This is a large and diverse, doubtfully natural subfamily divided in three tribes. It was found that all examined species invariably have vein C extensively setulose ventrally.

Tribe **Phaoniini** Malloch, 1917

A large tribe with currently 18 recognized genera; species from eight genera were examined (Table 1).

- *Metopomyia* Malloch, 1922, *Phaomusca* Malloch, 1926, *Pictia* Malloch, 1926, *Prohardya* Pont, 1969, *Souzalopesmyia* Albuquerque, 1951

The examined species of the above genera share the prevalent muscid state **A4** in which vein C is bare dorsally and extensively setulose ventrally: *Metopomyia atropunctipes* Malloch, 1922, *Phaomusca bakeri* Malloch, 1926, *Pictia xanthoceras* (Walker, 1859), *Prohardya* (3 spp) and *Souzalopesmyia singularis* (Stein, 1911).

- *Helina* Robineau-Desvoidy, 1830 (Fig. 13A–B)

Most of the 30+ species of *Helina* examined (including many unidentified ones from Australia) are without setulae dorsally on vein C (state **A4**, Fig. 13A). A few species stand out by having dorsal setulae on CS2 and CS3 or on CS3 only (state **A7**): *Helina allotalla* (Meigen, 1830) (Fig. 13B), *H. spinicosta* (Zetterstedt, 1845) and *H. pulchella* (Ringdahl, 1918). It was further observed that some female *H. quadrum* (Fabricius, 1805) and *H. vicina* (Czerny, 1919) have developed a short row of dorsal setulae on CS2 (state **A6**).

- *Lophosceles* Ringdahl, 1922

Most species examined have dorsal setulae on CS2 and CS3 only (state **A7**): *Lophosceles cinereiventris* (Zetterstedt, 1845), *L. impar* (Zetterstedt, 1845), *L. minimus* (Malloch, 1919) and *L. mutatus* (Fallén, 1825). Only *Lophosceles frenatus* (Holmgren, 1872) differs by having dorsal costal setulae on CS1–CS3 (state **A8**).

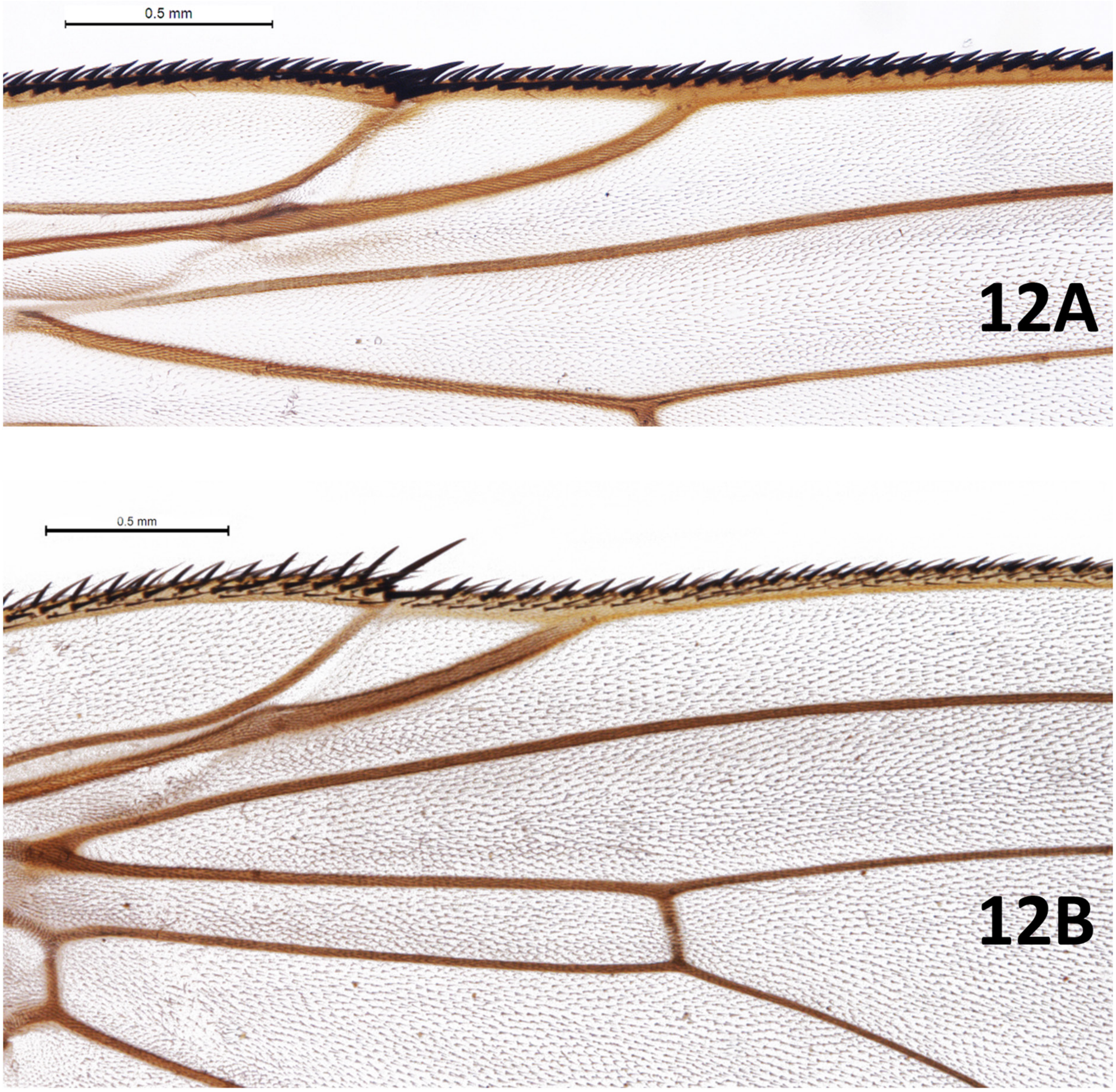

Fig. 12. ♀♀ of Muscidae Latreille, 1802. **A**. *Muscina stabulans* (Fallén, 1823), detail of wing showing CS1–3, dorsal view. **B**. *Palpibracus trivittatus* (Malloch, 1934), detail of wing showing CS1–3, dorsal view.

- *Phaonia* Robineau-Desvoidy, 1830 (Fig. 14A–D)

Most examined species of this large genus are without setulae dorsally on vein C (state **A4**): *Phaonia alpicola* (Zetterstedt, 1845), *P. angelicae* (Scopoli, 1763) (Fig. 14A), *P. apicalis* Stein, 1914, *P. asiatica* Hennig, 1963, *P. atronitens* Malloch, 1921, *P. aurata* Zinov'ev, 1992, *P. aureipollinosa* Xue & Wang, 1986, *P. bambusa* Shinonaga & Kano, 1971, *P. bambusella* Zinov'ev, 1992, *P. basisetosa* Zinov'ev, 1992, *P. bitincta* (Rondani, 1866), *P. boleticola* (Rondani, 1866) (males), *P. chalinata* (Pandellé, 1899), *P. cincta* (Zetterstedt, 1846), *P. consobrina* (Zetterstedt, 1838), *P. czernyi* Hennig, 1963, *P. errans* (Meigen, 1826), *P. exoleta* (Meigen, 1826), *P. flavomaculata* Malloch, 1921, *P. fuscicoxa* Emden, 1965, *P. gobertii* (Mik, 1881), some *P. gracilis* Stein, 1916, *P. halterata* (Stein, 1893), *P. himalaica* Zinov'ev, 1992, *P. hirtirostris* (Stein, 1907), *P. hybrida* (Schnabl, 1888), *P. impura* Zinov'ev, 1987, *P. incana* (Wiedemann, 1817), *P. kambaitiana* Emden, 1965, *P. kashmirensis* Malloch, 1921, *P. kobica* Schnabl in Schnabl & Dziedzicki, 1911, *P. laeta* (Fallén, 1823), *P. latipullatoides* Wang & Xue, 1997, *P. lugubris* (Meigen, 1826), *P. macroomata* Xue & Yang, 1998, *P. mediterranea* Hennig, 1963, *P. meigeni* Pont, 1986, *P. michelseni* Zinov'ev, 1992, *P. nitidula* Zinov'ev, 1992, *P. nymphaearum* (Robineau-Desvoidy, 1830), *P. pallidisquama* (Zetterstedt, 1849), *P. perdita* (Meigen, 1830), *P. pratensis* (Robineau-Desvoidy, 1830), *P. pura* (Loew, 1873), *P. regalis* (Stein, 1919), *P. rufipalpis* (Macquart, 1835), *P. rufivulgaris* Xue & Wang, 1989, *P. scutellata* (Zetterstedt, 1845) (except some females), *P. serva* (Meigen, 1826), *P. shanxiensis* Zhang *et al.*, 1985, *P. sordidisquama* Stein in Becker, 1908, *P. subfuscinervis* (Zetterstedt, 1838), *P. subventa* (Harris, 1780) (except some females), *P. sytschevskajae* Hennig, 1963, *P. thomsoni* Malloch, 1921, *P. trimaculata* (Bouché, 1834) (except some females), *P. tuguriorum* (Scopoli, 1763) (except some females), *P. valida* (Harris, 1780), some *P. villana* Robineau-Desvoidy, 1830 and *P. wahlbergi* Ringdahl, 1930.

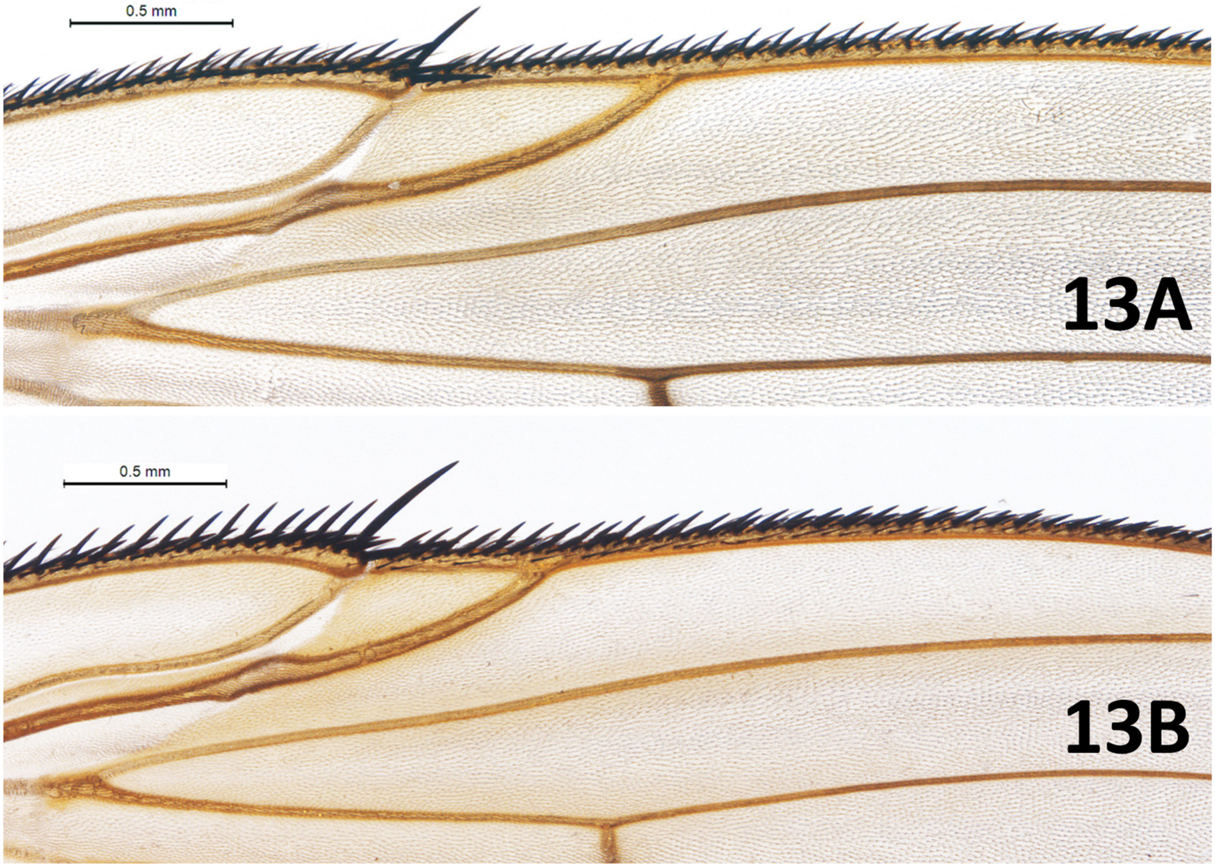

Fig. 13. ♀♀ of *Helina* Robineau-Desvoidy, 1830. **A**. *H. depuncta* (Fallén, 1825), detail of wing showing CS1–3, dorsal view. **B**. *H. allotalla* (Meigen, 1830), detail of wing showing CS1–3, dorsal view.

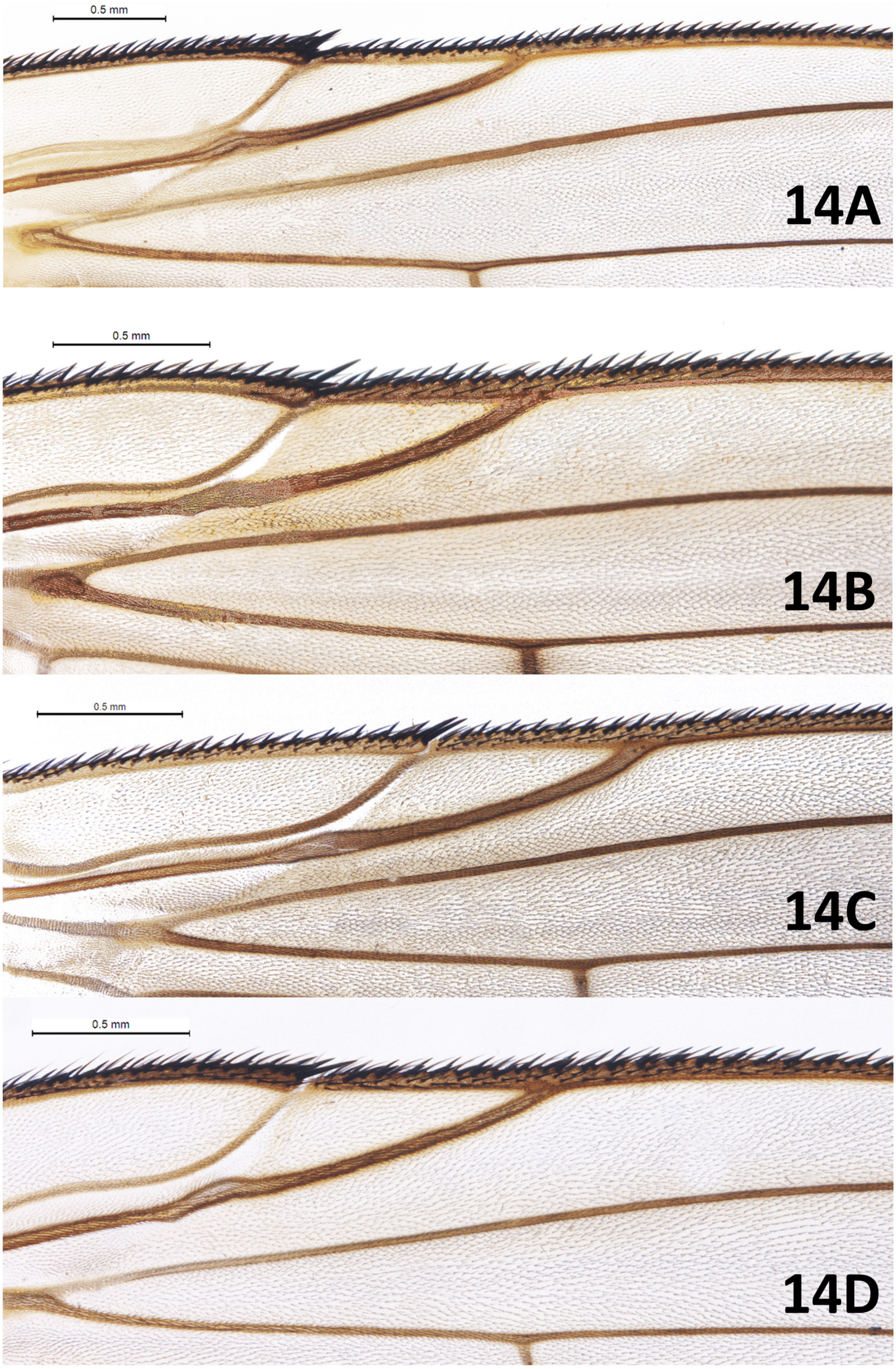

Fig. 14. ♀♀ of *Phaonia* Robineau-Desvoidy, 1830. **A**. *P. angelicae* (Scopoli, 1763), detail of wing showing CS1–3, dorsal view. **B**. *P. palpata* (Stein, 1897), detail of wing showing CS1–3, dorsal view. **C**. *P. rufiventris* (Scopoli, 1763), detail of wing showing CS1–3, dorsal view. **D**. *P. canescens* Stein, 1916, detail of wing showing CS1–3, dorsal view.

It was found that *Phaonia aeneiventris* (Zeterstedt, 1845), *P. amicula* Villeneuve, 1922, *P. boleticola* females, *P. canariensis* Villeneuve in Frey, 1936, *P. fuscata* (Fallén, 1825), some *P. gracilis*, some *P. incana*, *P. mystica* (Meigen, 1826), *P. nigrisquama* Stein in Becker, 1908, *P. palpata* (Stein, 1897) (Fig. 14B), some female *P. scutellata*, *P. subventa* (Harris, 1780), some female *P. trimaculata*, most *P. tuguriorum* (Scopoli, 1763) and some *P. villana* have a row of dorsal setulae confined to CS2 or sometimes extended onto the basal fifth of CS3 (state **A6**).

Most *Phaonia angulicornis* (Zetterstedt, 1838), *P. kowarzii* (Schnabl, 1887), some *P. longicornis* Stein, 1916, some *P. pallida* (Fabricius, 1787), *P. rufiventris* (Scopoli, 1763) (Fig. 14C), *P. steinii* (Strobl, 1898), *P. suecica* Ringdahl, 1947, *P. tiefii* (Schnabl, 1888) and *P. zugmayeriae* (Schnabl, 1888) have the dorsal costal setulae occupying CS2 and more than the basal half of CS3 (state **A7**).

The following species are extensively setulose dorsally on CS1–CS3 (state **A8**): *P. amabilis* (Meigen, 1826), *P. angulicornis* (some females), *P. atrocyanea* Ringdahl, 1916, *P. canescens* Stein, 1916 (Fig. 14D), *P. erronea* (Schnabl, 1887), *P. falleni* Michelsen, 1977, *P. jaroschewskii* (Schnabl, 1888), some *P. longicornis*, *P. magnicornis* (Zetterstedt, 1845), some *P. pallida* and *P. siebecki* Schnabl in Schnabl & Dziedzicki, 1911.

Phaonia angulicornis and *P. steinii* tend to have the setulae from the upper anterior spinule-setula row displaced dorsally on CS1.

Tribe **Eginiini** Stein, 1907 [Syllegopterini Brauer & Bergenstamm 1889]

Adult morphology and larval biology leave no doubt that this small tribe is monophyletic (Michelsen 2007). Species from two out of four recognized genera (Table 1) were examined.

- *Eginia* Robineau-Desvoidy, 1830, *Xenotachina* Malloch, 1921

The two examined species, *Eginia ocypterata* (Meigen, 1826) and *Xenotachina pallida* Malloch, 1921, have vein C extensively setulose dorsally (state **A8**). The same state expectedly applies to all eginiine genera and species.

Tribe **Dichaetomyiini** Emden, 1951

This is a relatively small tribe distributed primarily in the tropics of the Old World and Australia. Species from four of totally five recognized genera were examined (Table 1).

- *Aethiopomyia* Malloch, 1921, *Alluaudinella* Giglio-Tos, 1895, *Dichaetomyia* Malloch, 1921, *Ochromusca* Malloch, 1927

All examined species representing these genera reveal the prevalent muscid state in which vein C is bare dorsally and setulose ventrally (state **A4**): *Aethiopomyia patersoni* Zumpt, 1969, *A. steini* Curran, 1935, *Alluaudinella bivittata* (Macquart, 1843), *A. phasiaeformis* (Stein, 1906), *Dichaetomyia* (18 spp) and *Ochromusca secunda* Pont & Dear, 1976.

Subfamily **Mydaeinae** Verrall, 1888

The limits and monophyly of this subfamily, currently including 20 recognized genera, are far from settled. Species from 13 genera were examined (Table 1).

- *Afromydaea* Malloch, 1930, *Dimorphia* Malloch, 1922, *Graphomya* Robineau-Desvoidy, 1830, *Gymnopapuaia* Vockeroth, 1972, *Lasiopelta* Malloch, 1928, *Myospila* Rondani, 1856 (Fig. 15A), *Opsolasia* Coquillett, 1910, *Pseudohelina* Vockeroth, 1972, *Scutellomusca* Townsend, 1931

All examined species from these nine genera show the prevalent muscid state **A4** in which vein C is bare dorsally and extensively setulose ventrally: *Afromydaea geniculata* (Stein, 1913), *Dimorphia* (3 spp), *Graphomya* (6 spp), *Gymnopapuaia acuta* Vockeroth, 1972, *G. clavipalpis* Vockeroth, 1972, *Lasiopelta similis* Malloch, 1928, *Myospila* (25 spp), *Opsolasia orichalcea* (Zetterstedt, 1849), *Pseudohelina* (2 spp indet.) and *Scutellomusca scutellaris* (Fabricius, 1805).

- *Mydaea* Robineau-Desvoidy, 1830 (Fig. 15B–C)

All examined species are to a varying extent setulose dorsally on vein C.

The following species has a short, often irregular row of dorsal costal setulae confined to CS2, the basal part of CS3, or both (state **A6**): *Mydaea ancilla* (Meigen, 1826) (Fig. 15B).

The following species are extensively setulose dorsally on vein C except for a bare or practically bare C1 (state **A7**): *Mydaea anicula* (Zetterstedt, 1860), *M. corni* Scopoli, 1763, *M. deserta* (Zetterstedt, 1845), *M. detrita* (Zetterstedt, 1845), some *M. humeralis* Robineau-Desvoidy, 1830, *M. lateritia* (Rondani, 1866), *M. nubila* Stein, 1916, *M. obscurella* Malloch, 1921, *M. orthonevra* (Macquart, 1835), *M. palpalis* Stein, 1916, some *M. setifemur* Ringdahl, 1924 and *M. urbana* (Meigen, 1826).

The following species have a full row of dorsal costal setulae (state **A8**): *Mydaea affinis* Meade, 1891 (Fig. 15C), some *M. humeralis*, *M. nebulosa* (Stein, 1893), some *M. setifemur* and *M. sootryeni* Ringdahl, 1928.

- *Hebecnema* Schnabl, 1889 (Fig. 16A–B)

Most species examined, e.g., *H. umbratica* (Meigen, 1826) (Fig. 16A), have the prevalent muscid state **A4**, but *H. nigricolor* (Fallén, 1825) (Fig. 16B), as first noticed by Michelsen (2019), and one unidentified species from Tanzania deviate by having dorsal setulae on the basal two-thirds or more of CS3, and sometimes among females even some irregular dorsal setulae on CS2 (state **A7**).

- *Hemichlora* Wulp, 1896

The only included species, *Hemichlora scordalus* (Walker, 1861), has vein C extensively setulose dorsally (state **A8)**.

- *Gymnodia* Robineau-Desvoidy, 1863 (Fig. 16C)

Most of the 12 species examined show the prevalent muscid state **A4**, in which vein C is bare dorsally and extensively setulose ventrally, but a ventrally bare CS1 (state **A3**) was found in *Gymnodia subtilis* (Stein, 1909) (Fig. 16C) and a few other small-sized, unidentified *Gymnodia* spp of Afrotropical and Oriental origin.

Subfamily **Coenosiinae** Verrall, 1888

This large taxon is reasonably well defined and conceivably monophyletic (Couri & Pont 2000; Kutty *et al*. 2014). Among the two recognized tribes, Limnophorini and Coenosiini, only the latter is defined by alleged apomorphies. It was found that the great majority of the examined species representing 35 genera of Coenosiinae possess the prevalent muscid state **A4**, in which vein C is bare dorsally and extensively setulose ventrally.

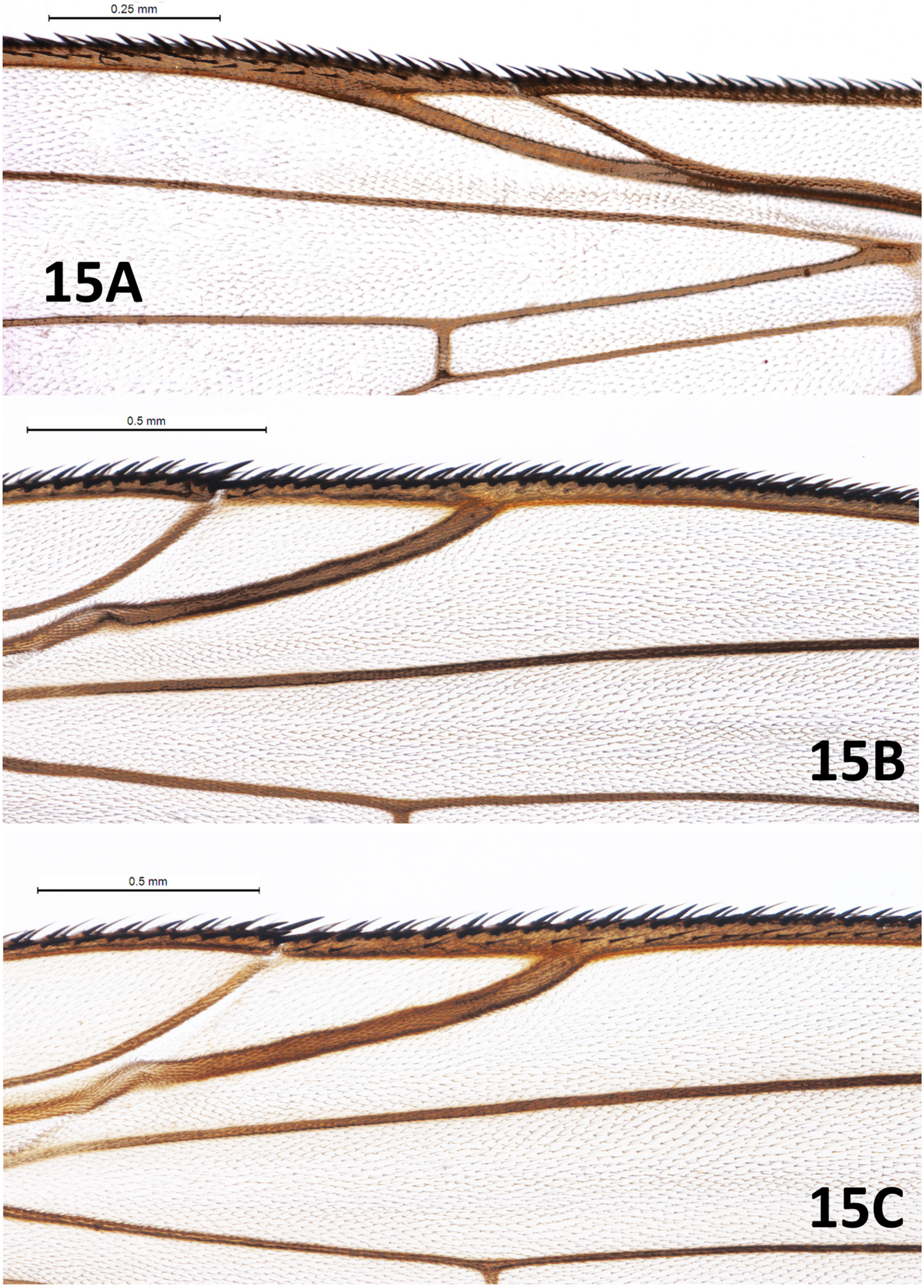

Fig. 15. ♀♀ of Muscidae Latreille, 1802. **A**. *Myospila bimaculata* (Macquart, 1834), detail of wing showing CS1–3, dorsal view. **B**. *Mydaea ancilla* (Meigen, 1826), detail of wing showing CS1–3, dorsal view. **C**. *M. affinis* Meade, 1891, detail of wing showing CS1–3, dorsal view.

Tribe **Limnophorini** Villeneuve, 1902

Species representing 12 out of a total of 24 currently recognized genera (Table 1) were examined.

- *Andersonosia* Emden, 1940, *Camptotarsopoda* Strand, 1913, *Heliographa* Malloch, 1921, *Limnophora* Robineau-Desvoidy, 1830, *Lispe* Latreille, 1797, *Lispoides* Malloch, 1920, *Neolimnophora* Schnabl, 1902, *Pachyceramyia* Albuquerque, 1955, *Villeneuvia* Schnabl & Dziedzicki, 1911

All examined species from these nine genera show the prevalent muscid state **A4**, in which vein C is bare dorsally and extensively setulose ventrally: *Andersonosia velutinifrons* (Malloch, 1928), *Camptotarsopoda* (3 spp), *Heliographa* (6 spp), *Limnophora* (30+ spp), *Lispe* (30+ spp), *Lispoides aequifrons* (Stein, 1898), *Neolimnophora maritima* (Röder, 1887), *N. virgo* (Villleneuve, 1906), *Pachyceramyia pantherina* (Wiedemann, 1824) and *Villeneuvia aestuum* (Villeneuve, 1902).

Deviations from state **A4** are unusual among limnophorine genera, but involve examples of both loss of ventral setulae and gain of dorsal setulae.

- *Spilogona* Schnabl, 1911

Examination of 40+ species of *Spilogona* revealed that the prevalent muscid state **A4** is the rule in this large genus, but Michelsen (2021) described *S. maderensis* from Madeira (Portugal), which exceptionally is setulose dorsally on vein C (state **A8**).

- *Tapantiomyia* Michelsen, 2017

The only species, *Tapantiomyia enigmatica* Michelsen, 2017, is in the male sex (female unknown) unique among Coenosiinae (Michelsen 2017: fig. 6) by the absence of ventral costal setulae, state **A0**, and further deviates from other Muscidae by the inflated CS1, which is bare except for a single anterior row of tiny, pale setulae.

- *Thaumasiochaeta* Stein, 1911 (Fig. 17A–B)

The examined four species of *Thaumasiochaeta* are setulose on the dorsal side of CS1 (state **A5**).

Tribe **Coenosiini** Verrall, 1888

A well defined, conceivably monophyletic tribe (Couri & Pont 2000), currently with 34 recognized genera; species from 23 genera were examined (Table 1).

- *Anaphalantus* Loew, 1857, *Apsil* Malloch, 1929, *Bithoracochaeta* Stein, 1911, *Brevicosta* Malloch, 1921, *Cephalispa* Malloch, 1935, *Limnospila* Schnabl, 1902, *Lispocephala* Pokorny, 1893, *Macrorchis* Rondani, 1877, *Neodexiopsis* Malloch, 1920, *Notoschoenomyza* Malloch, 1934, *Orchisia* Rondani, 1877, *Oxytonocera* Stein, 1919, *Parvisquama* Malloch, 1935, *Pseudocoenosia* Stein, 1916, *Pygophora* Schiner, 1868, *Reynoldsia* Malloch, 1934, *Schoenomyza* Haliday, 1833, *Schoenomyzina* Malloch,1934, *Spanochaeta* Stein, 1919, *Spathipheromyia* Bigot, 1884, *Stomopogon* Malloch, 1930

All examined species from these 21 genera show the prevalent muscid state **A4** in which vein C is bare dorsally and extensively setulose ventrally: *Anaphalantus longicornis* (Macquart, 1843), *Apsil* (7 spp), *Bithoracochaeta* (4 spp), *Brevicosta* (1 sp. indet.), *Cephalispa* (1 sp. indet.), *Limnospila albifrons* (Zetterstedt, 1849), *Lispocephala* (10 spp), *Macrorchis meditata* (Fallén, 1825), *Macrorchis* sp. indet., *Neodexiopsis* (3 sp. indet.), *Notoschoenomyza sulfuriceps* Malloch, 1934, *Notoschoenomyza* sp. indet., *Orchisia costata* (Meigen, 1826), *Oxytonocera nigrohalterata* (Stein, 1904), *Parvisquama* (3 spp indet.), *Pseudocoenosia abnormis* Stein, 1916, *P. solitaria* (Zetterstedt, 1838), *Pygophora* (7 spp),

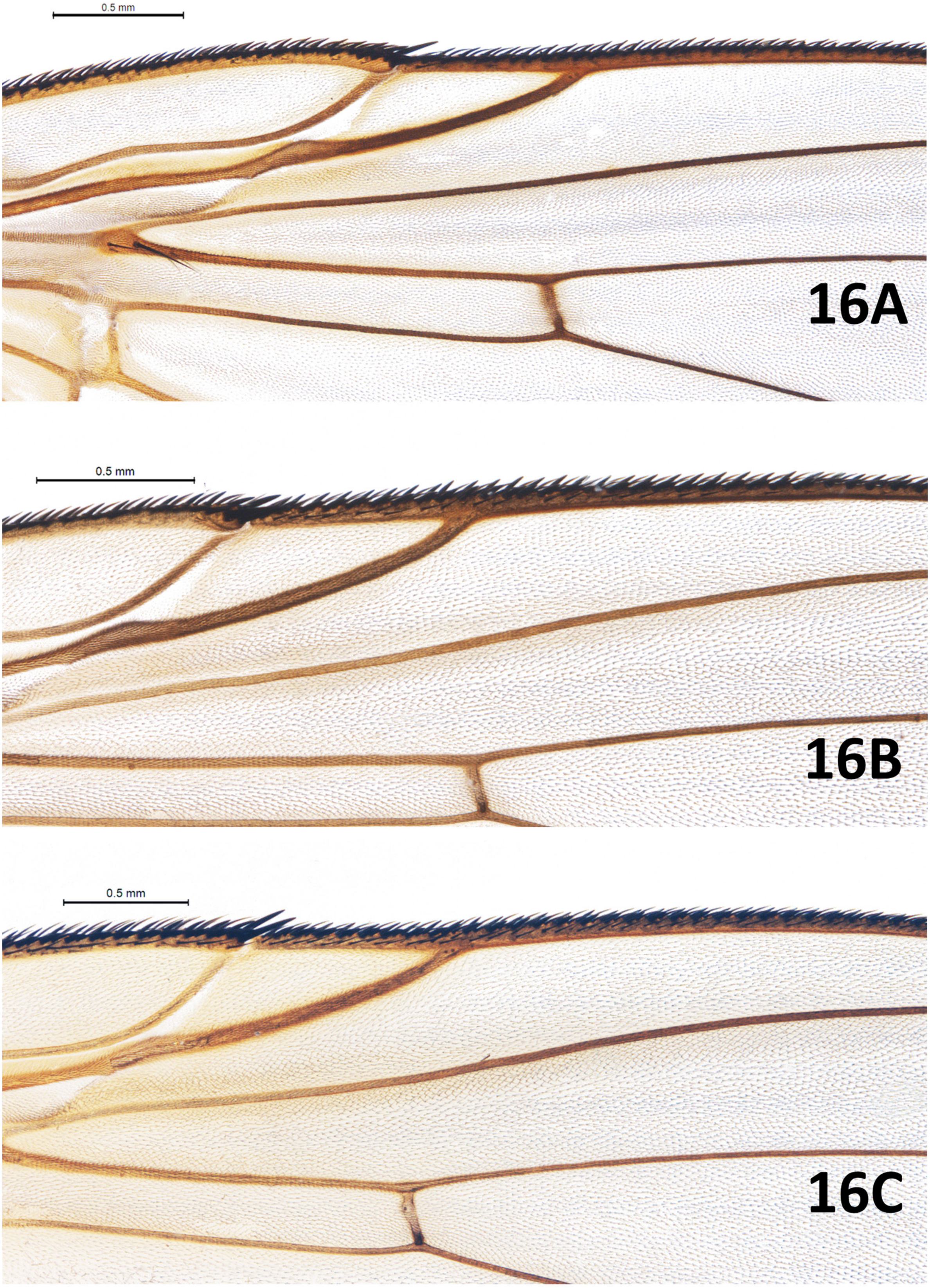

Fig. 16. ♀♀ of Muscidae Latreille, 1802. **A**. *Hebecnema umbratica* (Meigen, 1826), detail of wing showing CS1–3, dorsal view. **B**. *H. nigricolor* (Fallén, 1825), detail of wing showing CS1–3, dorsal view. **C**. *Gymnodia subtilis* (Stein, 1909), detail of wing showing CS1–3, ventral view.

Reynoldsia (3 spp), *Schoenomyza* (3 spp), *Schoenomyzina triangularis* Malloch, 1934, *Schoenomyzina* sp. indet., *Spanochaeta dorsalis* (Roser, 1840), *Spathipheromyia atra* Malloch, 1934, *S. guttipennis* (Thomson, 1869), *Stomopogon albiseta* (Stein, 1911) and *S. inculta* (Stein, 1911).

The examined species of *Neodexiopsis*, *Orchisia* and *Spathipheromyia* have the setulae from the lower anterior spinule-setula row displaced dorsally, so that they occupy the usually bare strip separating the spinule-setula rows.

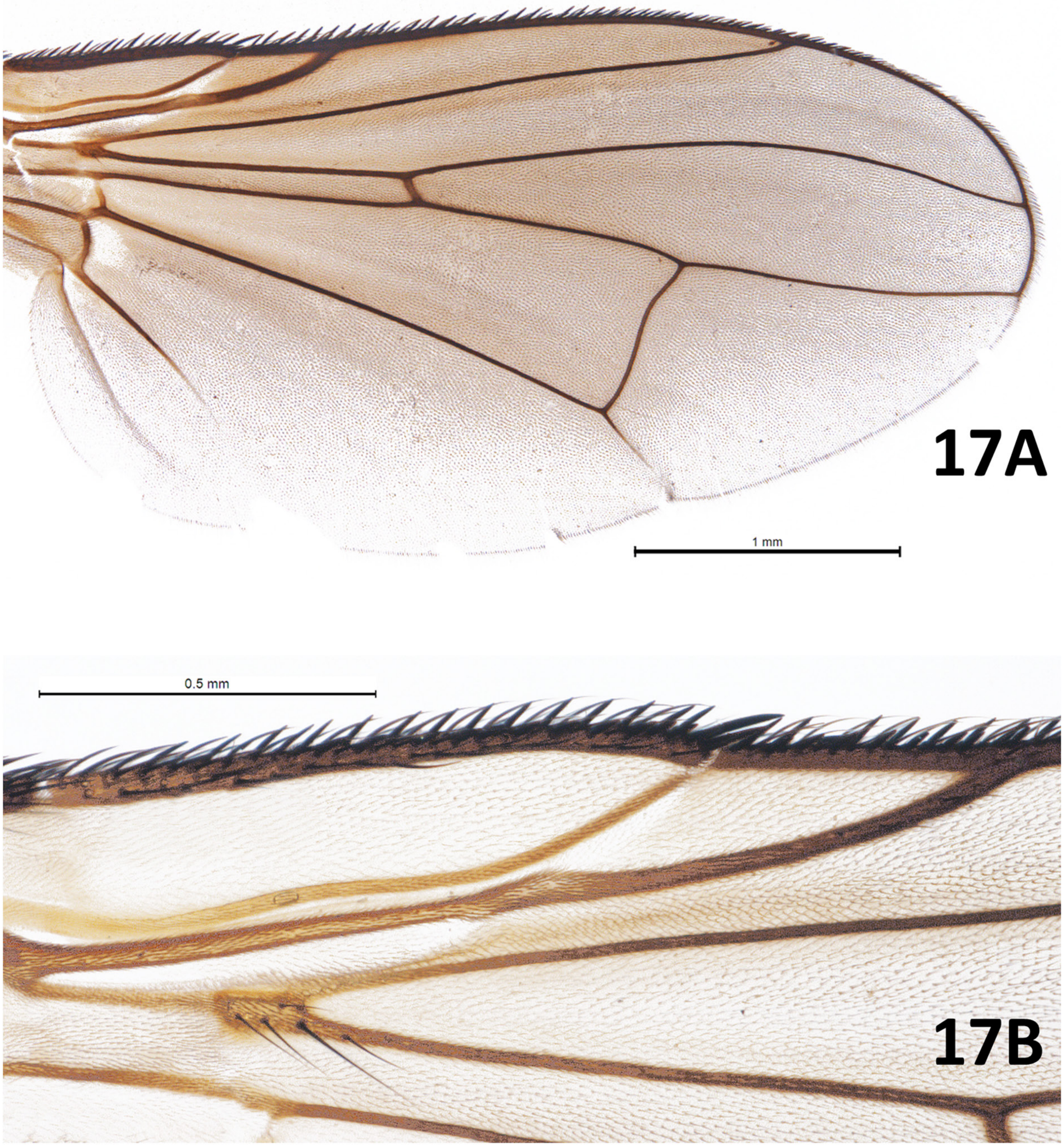

Fig. 17. ♀ of *Thaumasiochaeta* Stein, 1911. **A**. Wing, dorsal view. **B**. Detail of wing showing CS1–2, dorsal view.

- *Coenosia* Meigen, 1826 (Figs 1A–B, 18A–D)

The examined 50+ species of *Coenosia* all show the prevalent muscid state **A4** in which vein C is bare dorsally and extensively setulose ventrally (Figs 1A–B, 18A–C). One exception was found in the boreal Palearctic species *Coenosia emiliae* Lukasheva, 1986 (Fig. 18D), which has dorsal costal setulae occupying CS2 and CS3 (state **A7**).

- *Cordiluroides* Albuquerque, 1954

The examined species, *Cordiluroides bistriata* (Wulp, 1896) and *Cordiluroides* sp. indet., agree with *Coenosia emiliae* in having setulae dorsally on CS2 and CS3 in addition to the mandatory ventral costal setulae (state **A7**).

Discussion

Phylogenetic and taxonomic implications

The monophyly of the present families Fanniidae and Muscidae is well supported by morphological (Chillcott 1961; Hennig 1965; Michelsen 2007; Domínguez & Roig-Juñent 2008) and molecular evidence (Kutty *et al*. 2014). Molecular studies attempting to illucidate relationships within the Calyptratae support that the major dichotomies took place in the following order (Kutty *et al*. 2008, 2019): Hippoboscoidea (louse flies, bat fly families and tsetse flies), Fanniidae, Muscidae, Anthomyiidae-Scathophagidae, Oestroidea. Until recently, the Oestroidea consisted of the families Ulurumyiidae, Mesembrinellidae, Tachinidae, Polleniidae, Rhinophoridae, Calliphoridae, Rhiniidae, Mystacinobiidae, Oestridae and Sarcophagidae (Kutty *et al.* 2019). However, a brand new proposal by Yan *et al.* (2021) resulting from a comprehensive phylogenomic analysis redefines the blowflies (Calliphoridae) by downgrading the former Rhinophoridae and Rhiniidae to subfamilies of Calliphoridae.

Fanniidae

The costal chaetotaxy is remarkably uniform throughout the family Fanniidae. It consists of two parallel anterior rows of alternating spinules and setulae, as is the typical pattern in calyptrate flies other than Hippoboscoidea (Hackman & Väisänen 1985), but without additional ventral and dorsal setulae (state **A0**) other than the standard dorsal row of gustatory sensilla. Expectedly, the monobasic fanniid genus *Zealandofannia* described by Domínguez & Pont (2014) exhibits the same costal state.

Only *Australofannia*, known for two Australian endemic species, has a deviating and clearly derived costal chaetotaxy involving extensive replacement of the usual spinules by setulae and development of setulae ventrally and dorsally on vein C (state **A8**). A similar pattern is rarely seen in the major calyptrate radiation forming the sister group of Fanniidae, but has evidently been attained twice, in Scathophagidae and Oestridae. One other, less conspicuous deviation from the usual costal chaetotaxy in fanniids concerns the ‘false’ ventral and dorsal setulae on CS1 (Fig. 2D) here observed in two species of *Piezura*. This may prove autapomorphic for *Piezura*, a genus with only five recognized species (Moores & Savage 2005).

There is no mention of the strange costal chaetotaxy of *Australofannia* in the description of the genus (Pont 1977) or in the morphology-based analysis of Fanniidae by Domínguez & Roig-Juñent (2008). It seems that the only focus on the costal chaetotaxy in the taxonomic literature on Fanniidae has been on the relative size of the costal spine at the subcostal break. Incidentally, this ‘spine’ consists of two subequal spines, one from each of the anterior spinule-setula rows. Normally, these spines are short and inconspicuous (Fig. 2B–D), but quite strong in one species of *Piezura* as pointed out by Hennig (1955a, 1955b) and Chillcott (1961).

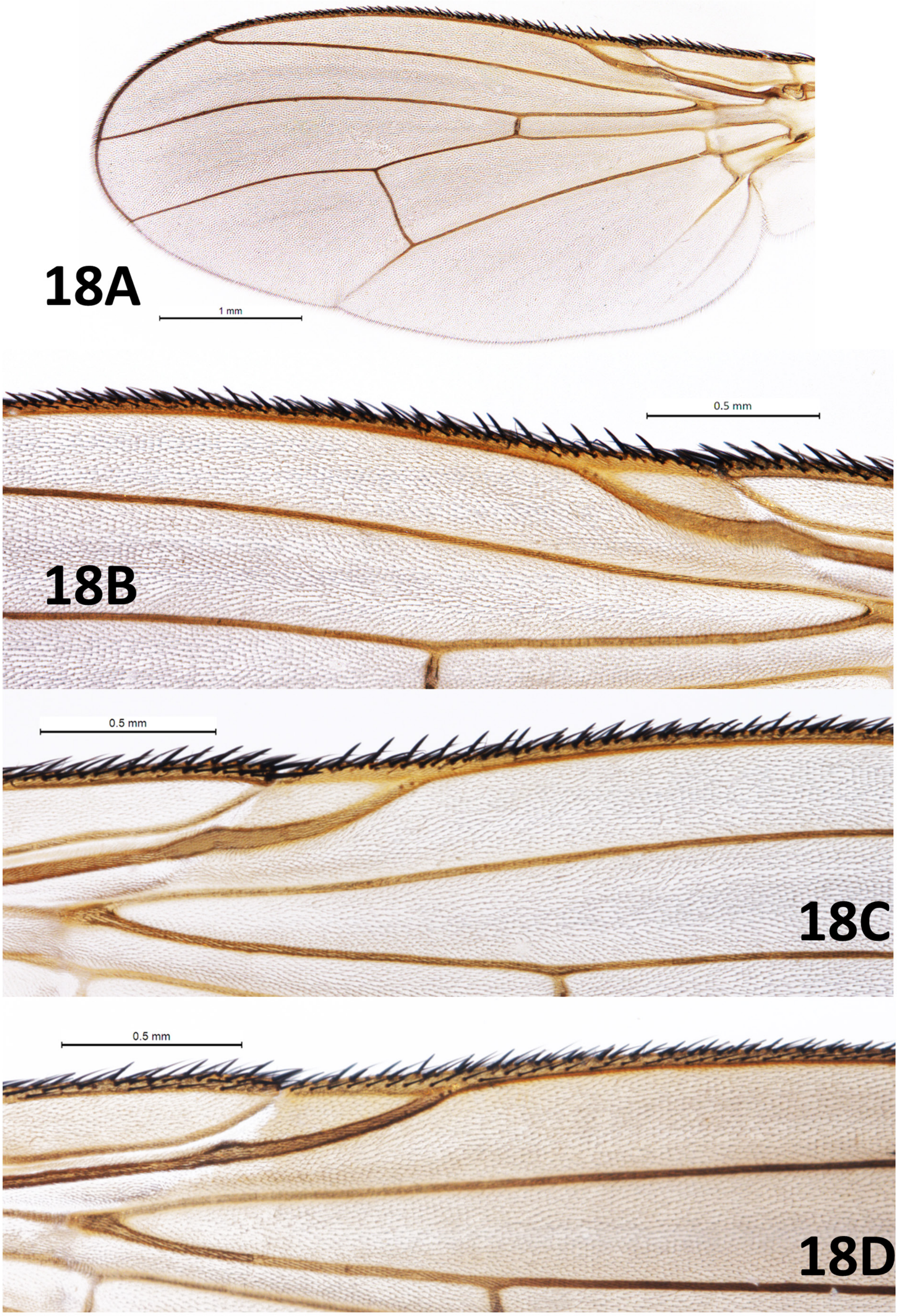

Fig. 18. ♀♀ of *Coenosia* Meigen, 1826. **A**. *C. intermedia* (Fallén, 1825), wing, ventral view. **B**. Same, detail of wing showing CS1–3, ventral view. **C**. Same, detail of wing showing CS1–3, dorsal view. **D**. *C. emiliae* Lukasheva, 1986, detail of wing showing CS1–3, dorsal view.

Muscidae

Two recent molecular analyses of the Muscidae by Kutty *et al.* (2014) and Haseyama *et al.* (2015) reveal major disagreements with respect to the basic muscid radiation and relationships. Both analyses challenge current morphology-based proposals on how to classify this comprehensive clade in subfamilies and tribes. It is expected that larger and more refined molecular analyses, combined with or corroborated by morphology, will eventually lead to more stability in the higher classification of the Muscidae.

The present study revealed that the costal chaetotaxy in Muscidae is very diverse with respect to character **A (**development and distribution of ventral and dorsal setulae), as this varies through all states (**A0–A8**) described above. It also disclosed that state **A4** (vein C extensively setulose ventrally and wholly bare dorsally) is very prevalent and found to be present in all muscid subfamilies and tribes apart from the small and uniform Atherigoninae and Eginiini (Table 1). This allows two assumptions: (1) **A4** represents the ancestral state in Muscidae in contrast to the assumed ancestral state **A0** in Fanniidae, and (2) the main transformation of character **A** during muscid radiation has been bi-directional, one leading to a loss of the ventral costal setulae (states **A3→A0**), the other leading to a gain of dorsal costal setulae (states **A5→A8**).

The dominant muscid state **A4** may be present invariably in most genera of Muscidae including the specious *Dichaetomyia*, *Myospila*, *Limnophora*, *Lispe* and *Pygophora*. State **A4** is also the rule in *Thricops*, *Helina*, *Phaonia*, *Gymnodia*, *Hebecnema*, *Spilogona* and *Coenosia*, but these genera contain one or more species with a deviating costal chaetotaxy

Absence of ventral costal setulae is basic to the Atherigoninae, and a main trend towards reduction of ventral costal setulae is seen in the Azeliinae and Muscinae (Muscini, Stomoxyini). Exceptions to this are *Huckettomyia* and some *Thricops* (Azeliini) that have attained dorsal setulae on vein C.

A main trend towards gain of dorsal costal setulae is seen in the Reinwardtiinae, Cyrtoneurininae, Phaoniinae (Phaoniini, Eginiini), Mydaeinae and Coenosiinae (Limnophorini, Coenosiini). Loss of ventral costal setulae is exceedingly rare in these subfamilies, presently observed only in *Synthesiomyia nudiseta* (Reinwardtiinae), some *Gymnodia* (Mydaeinae) and *Tapantiomyia enigmatica* (Coenosiinae).

Leaving aside the in many ways aberrant Atherigoninae, the above subdivision of the Muscidae determined by opposite transformations of character **A** coincides with the basal split of the family advocated by Kutty *et al.* (2014) on basis of molecular data.

A transformation of character **A** in terms of loss of ventral costal setulae is seen within the genera *Hydrotaea*, *Musca*, *Neomyia*, *Polietes*, *Haematobia*, *Haematobosca*, *Stomoxys* and *Gymnodia*. As would be expected, the most ancestral species of *Hydrotaea*, as judged from the larval mouth skeleton, number of instars and feeding habits (Skidmore 1985; Grzywacz 2013), are those without or with only a moderate loss of ventral costal setulae (states **A4**, **A2**). The opposite trend in terms of gain of dorsal costal can be observed in the genera *Thricops*, *Helina*, *Phaonia*, *Hebecnema*, *Spilogona* and *Coenosia*. To the extent that the genera listed above are monophyletic, it seems safe to regard **A4** as the ancestral state, except for the genus *Musca* starting out with state **A2**.

One case of character state reversal was found in *Drymeia*, a large genus characterized by the absence of ventral costal setulae (state **A0**). Only *Drymeia hamata* was found to have a ventrally setulose vein C (state **A4**), which is the prevailing and ancestral state in most muscid lineages but not in *Drymeia*, as proboscis morphology (Michelsen 2011) and molecular evidence (Savage & Sorokina 2021) place *D. hamata* in a subordinate position within *Drymeia*.

Males and females of the same species normally agree with respect to character **A**. Exceptionally, as seen in some species of *Thricops*, *Helina* and *Phaonia*, the dorsal costal setulae are more abundant or confined to the female sex or to some female specimens. In *Pyrellia* a stable difference determined by gender was found in the distribution of the ventral costal setulae. Within-species variation of character **A** not determined by gender is unusual, but was found in a few species of *Thricops*, *Helina*, *Phaonia* and *Mydaea*.

In the following are given some examples illustrating the practical use of the costal chaetotaxy, in particular character **A**, in systematic work on Muscidae.

Azelia and *Thricops* are the only genera with setulae at the inner hind margin of the hind coxae. These genera are easily separated by vein C, which is bare ventrally in *Azelia* but setulose ventrally in *Thricops*. As discussed by Zielke (2016), *Spilogona* includes several densely setose species that on external facies resemble and have been confused with species of *Drymeia*, albeit these genera are distantly related. However, the present study revealed that vein C on the ventral side is setulose in *Spilogona* and bare in *Drymeia*. Only *D. hamata*, a species with strikingly long and slender labella (Michelsen 2011), agrees with *Spilogona* by having ventral costal setulae. Zielke (2016) described a second species of *Drymeia* with extended labella, but it remains to be determined whether it is bare or setulose on the ventral side of vein C.

The presence of dorsal costal setulae in *Huckettomyia*, a detail overlooked in the existing treatments of the genus (Pont & Shinonaga 1970; Savage & Wheeler 2004; Pont 2005; Pont & Vikhrev 2009), may help to distinguish females of this genus from habitually similar species of *Hydrotaea* and *Neohydrotaea*.

The Stomoxyini include at least three genera (*Haematobia*, *Haematobosca* and *Stomoxys*) in which differences in the distribution of ventral costal setulae (**A4**, **A3**, **A1**) may help to separate similar species. This character received no attention in the World revision of Stomoxyini by Zumpt (1973).

Species of *Atherigona* are readily distinguished from superficially similar species of Coenosiini by the absence of ventral setulae on vein C (state **A0**).

Major disagreements prevail in how to define and delimit the Reinwardtiinae and Cyrtoneurininae in order to attain monophyly (Couri & de Carvalho 2003; Schuehli & de Carvalho 2005; Soares 2008; Savage 2009; Haseyama & de Carvalho 2011, 2012; Patitucci *et al.* 2011; Pereira-Colavite & de Carvalho 2012; Kutty *et al.* 2014; Haseyama *et al.* 2015, 2019; Pérez *et al.* 2020). Both subfamilies contain many small Neo- and Afrotropical genera with unsettled relationships. It was observed here that the Reinwardtiinae and Cyrtoneurininae as presently delimited both include genera that have vein C either bare or extensively setulose dorsally, an aspect that perhaps deserves more attention in future studies on these problematic groups.

The examined species of *Thaumasiochaeta* have dorsal setulae on CS1 (Fig. 17A–B). This costal chaetotaxy (state **A5**) is unique among the examined genera of Limnophorini.

Both examined species of the small Neotropical genus *Cordiluroides* have dorsal costal setulae on CS2 and CS3 (state **A7**). This is an unusual and derived state within the Coenosiinae (presently seen elsewhere in *Coenosia emiliae*) that may help to characterize and distinguish *Cordiluroides* from allied genera, provided it turns out to be stable at the species level.

Conclusions

There exist numerous morphology-based studies attempting to reveal phylogenetic relationships within the Fanniidae and Muscidae at family-group or genus level. These contain as a rule a list of variable, two- or multi-state characters considered relevant for scoring in a selection of species. My search through such character lists revealed that these often include characters from the wing chaetotaxy, but practically never from the chaetotaxy of the costal vein. Only an analysis of the Muscini by Nihei & de Carvalho (2007) includes a three-state character describing variation in the development of setulae on the ventral side of vein C, i.e., equivalent to character **A**. In a follow-up by Nihei & de Carvalho (2009) treating the genus-group taxa of Muscini in a key and by individual diagnoses the state of the ventral costal setulae is only mentioned for *Mesembrina* and *Pyrellia*.

It seems safe to conclude that the present comparative study of the costal chaetotaxy in Fanniidae and Muscidae has paid off by disclosing a wealth of previously unnoticed character data and patterns of immediate use in various systematic contexts.

Uluru macalpinei (Ulurumyiidae), a possible sister species of the remaining ca 15000 species of Oestroidea (Kutty *et al.* 2019), is extensively setulose on both sides of vein C (state **A8)** according to Michelsen & Pape (2017). That family aside, it seems that information about character **A** in the oestroid flies is fragmentary or missing for several groups. Observations made on the NW European fauna of blowflies (Calliphoridae s. lat.) by Rognes (1992) suggest that character **A** is a powerful diagnostic tool at the family-group level: Rhiniinae **A0**, Chrysomyinae **A2**, Polleniinae [now Polleniidae] **A2**, Helicoboscinae [now in Ameniinae] **A2**, Calliphorinae **A1–A2** (ventral costal setulae on CS1 + CS2), Luciliinae **A4**, Melanomyinae [now in Calliphorinae] **A4**. It remains to be determined to what extent these scores hold for the World fauna of blowflies. A targeted comparative study of the chaetotaxy of vein C, especially character **A**, in the remaining oestroid families – other than the apterous Mystacinobiidae – thus seems rewarding.

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