BAMBOO-STEM FLIES: AN ANNOTATED KEY TO THE SPECIES OF THE SOPHIRA COMPLEX OF GENERA (DIPTERA: TEPHRITIDAE: ACANTHONEVRINI)

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Abstract

Indo-Australian and East Asian fruit flies placed in the Sophira complex of genera are reviewed and keyed. The 63 recognised species are referred to 25 genera: Adramoides Hardy (1 sp.), Antisophira Hardy (1 sp.), Cleitamiphanes Hering (1 sp.), Colobostrella Hendel, stat. rev. (= Saucromyia Hardy, syn. n.) (4 spp); Colobostroter Enderlein (1 sp.), Enicopterina Malloch (1 sp.), Exallosophira Hardy (1 sp.), Felderimyia Hendel (3 spp), Homoiothemara Hardy (1 sp.), Kambangania de Meijere (3 spp), Langatia Hancock & Drew (1 sp.), Loriomyia Kertész (1 sp.), Parasophira Hardy, stat. rev. (1 sp.), Phorelliosoma Hendel (6 spp), Polyara Walker (3 spp), Polyaroidea Hardy (3 spp), Proptilona Zia, stat. rev. (= Heterosophira Hardy, syn. n., = Spaniothrix Hardy, syn. n.) (4 spp), Pseudacrotoxa Hering (1 sp.), Pseudosophira Malloch (1 sp.), Robertsomyia Hardy (1 sp.), Seraca Walker, stat. rev. (3 spp), Soosina Hering (2 spp), Sophira Walker (11 spp), Terastiomvia Bigot (3 spp) and Tritaeniopteron de Meijere (5 spp). Proptilona disjuncta (Hardy), comb. n. and P. vittata (Hardy), comb. n. are transferred from Kambangania and P. uncinata (Hering), comb. n. is transferred from Acanthonevra Macquart. Colobostrella bicolor (Hardy), comb. n. and C. spectabilis (Hardy), comb. n. are transferred from Saucromyia and Sophira respectively. Seraca longiplaga (Hering) is placed as a new synonym of S. signifera Walker. Sophira insueta Hering is placed as a new synonym of S. limbipennis (van der Wulp) and Sophira borneensis Hering, stat. n. is raised to species from a subspecies of S. limbata Enderlein.

Introduction

Indo-Australian fruit flies show a great diversity of larval hosts. While many breed in fruits or flowers and some beneath the bark of trees, many others develop in the shoots or stems of bamboo (Poaceae: Bambusoideae). Young, developing bamboo shoots are used by most genera in the dacine tribe Gastrozonini (Hancock and Drew 1999), while several genera in the *Acanthonevra* group of the phytalmiine tribe Acanthonevrini (*sensu* Korneyev 1999) are also known to utilise this host (Hancock and Drew 1995a, b). In the *Acanthonevra* complex of genera within this group, larvae of *Rioxoptilona* Hendel use decaying bamboo shoots while those of *Ptilona* van der Wulp develop in the internodes of dead bamboo culms (Hancock 2011b). Larvae in the related *Sophira* complex, however, appear to use living bamboo, developing in the internodes of older shoots or stems.

Hardy (1980) included the following genera within his Sophira group: Sophira Walker, Exallosophira Hardy, Tritaeniopteron de Meijere, Dacopsis Hering and Xenosophira Hardy. Korneyev (1999) referred Xenosophira to Tribe Phascini and recognised an expanded Sophira complex, placing it in his Ptilona subgroup of the Acanthonevra group and including the following genera: Sophira, Soosina Hering, Kambangania de Meijere, Loriomyia Kertész, Felderimyia Hendel, Antisophira Hardy, Exallosophira, Langatia Hancock & Drew, Cleitamiphanes Hering and possibly Colobostroter Enderlein, Terastiomyia Bigot and Pseudosophira Malloch.

Hancock and Drew (2003) excluded *Dacopsis* from the *Sophira* complex and included *Loriomyia* (= *Agnostophana* Hering) and *Stymbara* Walker from New Guinea, *Exallosophira* from Solomon Islands and *Enicopterina* Malloch from Fiji. Two further genera, *Adramoides* Hardy from Thailand and *Robertsomyia* Hardy from Papua New Guinea, were added by Hancock and Drew (2005) and Hancock (2005) respectively. *Stymbara* was subsequently transferred to the *Acanthonevra* subgroup by Hancock (2005).

Homoiothemara Hardy, Phorelliosoma Hendel, Polyara Walker, Polyaroidea Hardy and Pseudacrotoxa Hering are here added to the Sophira complex, while Parasophira Hardy is raised from subgeneric level and Colobostrella Hendel (= Saucromyia Hardy), Proptilona Zia and Seraca Walker are reinstated from synonymy.

This is a group of often large-sized flies (wing and body lengths 5-16 mm), with the antennal arista normally long-plumose (pubescent in *Phorelliosoma*) and with 2 or 3 pairs of scutellar setae, the middle (secondary) pair distinct, vestigial or absent. The stigma and/or wing cell c are often elongate and the scutum, while often with 2 or 4 dark longitudinal vittae, usually lacks a dark medial vitta. Presutural setae are often absent. The complex is restricted to the Oriental and Indo-Australian Regions, being well represented in Sundaland (Peninsular Malaysia, Sumatra, Java and Borneo), where nine genera and 22 species are recorded. Four endemic genera occur in Sulawesi, two in the southern Philippines, five in New Guinea and one each in the Solomon Islands and Fiji.

In order to aid identification of the 25 genera and 63 species now included in the *Sophira* complex, an annotated key is provided below, updating the partial keys of Hardy (1973, 1974, 1980, 1986a, b, 1988) and Wang (1998), where illustrations of most species may be found. Generic limits generally follow Norrbom *et al.* (1999) except where noted otherwise. Additional sources for illustrations are indicated in the key.

An unrelated species, *Euphranta chrysopila* Hendel (Trypetinae: Adramini), has been collected on bamboo stems in Taiwan and might be mistaken for a member of the *Sophira* complex. It is easily recognised by the presence of long hairs on the anatergite and the wing pattern (largely yellow anteriorly and hyaline posteriorly with a broad black apex and two transverse black bands: see Hendel 1913). Similarly, the slender, black-bodied *Euphranta macularis* (Wiedemann) (= *striatella* van der Wulp) has been collected on *Dendrocalamus brandisii* trunks in southern Thailand (Permkam 2005). It is likely that both species were visiting bamboo to feed on algal or fungal growths rather than to use it as a larval host.

Biology of Sophira-complex flies

Little is known of the biology of these flies. Sophira borneensis Hering (as S. limbata Enderlein) was collected on the bark of felled trees in Sarawak

(Perkins 1938), while Hardy (1980, 1986b, 1988) collected Cleitamiphanes heinrichi Hering, Colobostrella spectabilis (Hardy), Seraca linduensis (Hardy), Terastiomvia distorta (Walker) and T. lobifera Bigot on foliage of groundcover plants in dense rainforest in Sulawesi. Tritaeniopteron tetraspilotum Hardy was collected at cut shoots of the bamboo Thyrostachys oliveri in southern Thailand (Permkam 1995). Felderimyia flavipennis Hancock & Drew, F. fuscipennis Hendel, F. gombakensis Hancock & Drew, Langatia setinerva Hancock & Drew and Kambangania vpsilon (Rondani) were collected at cut bamboo shoots in Malaysia (Hancock and Drew 1994, 1995b, D. Kovac and P. Dohm pers. comm.). Felderimvia gombakensis was collected on various species of Bambusa, Dendrocalamus, Gigantochloa and Cephalostachyum in Thailand or Malaysia (Dohm et al. 2008), while F. fuscipennis was collected on stems of Dendrocalamus membranaceus and D. strictus in southern Thailand (Permkam 2005). A detailed account of the biology of Felderimyia species, particularly F. gombakensis, may be found in Dohm et al. (2008).

The only confirmed breeding records for Sophira complex species are from the stems or internodes of living bamboo. Felderimyia gombakensis was reared from the internodal spaces of shoots of the bamboos Gigantochloa scortechinii and G. latifolia in West Malaysia and Cephalostachyum pergracile in northern Thailand, the larvae entering the internodes of older bamboo shoots through holes made by larvae of Lasiochila Weise beetles (Chrysomelidae: Hispinae), living semi-aquatically in the water body of the internodal cavity and feeding on detritus or microbial growth (Dohm et al. 2008). Langatia setinerva was bred once from the water-filled internodes of a fallen, rotting shoot of Gigantochloa scortechinii (Dohm et al. 2008, 2010) that was presumably still alive when infested. Robertsomyia paradoxa Hardy was reared from the stems of live Bambusa sp. in Castanopsis (oak) forest (Hardy 1983), Polyara bambusae Hardy from 'young shoots of living Bambusa; the larvae tunnel within the stems of young shoots causing the death of the newly opened leaves' (H. Roberts, cited in Hardy 1986) and Pseudacrotoxa appendicigera Hering from the shoots of native Bambusa by Hardy (1988), all in Papua New Guinea.

Revised and reinstated genera

Colobostrella Hendel, 1914, stat. rev.

(= Saucromyia Hardy, 1986, syn. n.)

Placed as a synonym of *Sophira* by Hardy (1980) but apparently closer to *Seraca* and reinstated here to include four species from Sulawesi. The wing and scutal patterns differ significantly from those of *Sophira* and related genera; the hyaline indentation from costa enclosing R-M crossvein is an unusual character shared with *Cleitamiphanes*, *Homoiothemara* and *Seraca*. I am unable to find any characters significant enough to separate *Saucromyia* from *Colobostrella* and regard them as synonyms; *C. spectabilis* forms a link

between them and the presence or absence of a transverse hyaline indentation in cell m is seen also in *Kambangania*.

Species: bicolor (Hardy), comb. n. [ex Saucromyia]; bistriga (Walker), [ex Sophira]; plagifera (Walker), (= ruficauda Hendel) [type species] [ex Sophira]; spectabilis (Hardy), comb. n. [ex Sophira].

Kambangania de Meijere, 1914

Formerly included as a subgenus of *Sophira* and reinstated as a genus by Korneyev (1999); here modified to include three Sundaland species that lack both katepisternal and presutural acrostichal setae and have distinctive wing and scutal markings and a concave face; in two species (*K. metatarsata* and *K. ypsilon*) the mid basitarsus is modified in males.

Species: metatarsata de Meijere [type species] (Fig. 1); simillima (Hering); ypsilon (Rondani) (= disjuncta Hardy).

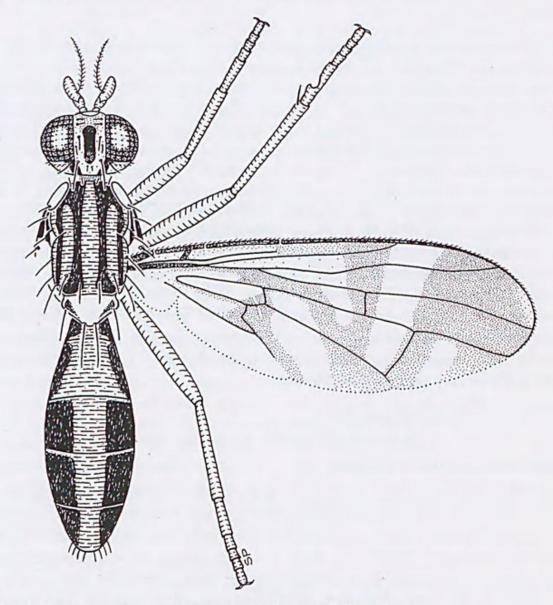


Fig. 1. Kambangania metatarsata de Meijere: male from Java.

Parasophira Hardy, 1980, stat. rev.

Established as a subgenus of *Sophira* by Hardy (1980) and here treated as a genus to include a single species from Borneo that cannot confidently be referred to any other recognised genus. It appears closest to *Kambangania* and has a similarly concave face but both katepisternal and presutural acrostichal setae are present and the wing, scutal and abdominal markings are distinctive. *Colobostrella*, *Seraca*, *Soosina* and *Sophira* have the katepisternal setae absent or vestigial, the presutural setae present and a vertical face.

Species: concinna (Walker) [type species] (Fig. 2).

Colobostrella biangulata de Meijere, described from Sumatra (de Meijere 1924) and placed in Sophira (Parasophira) by Hardy (1980), was transferred to Paraphasca Hardy (Tribe Phascini) by Hancock (2011a). 'Sophira (Parasophira) sp. related to concinna' of Hardy (1988) is a misidentification of Rioxoptilona shinonagai (Hardy) in the Acanthonevra complex of genera.

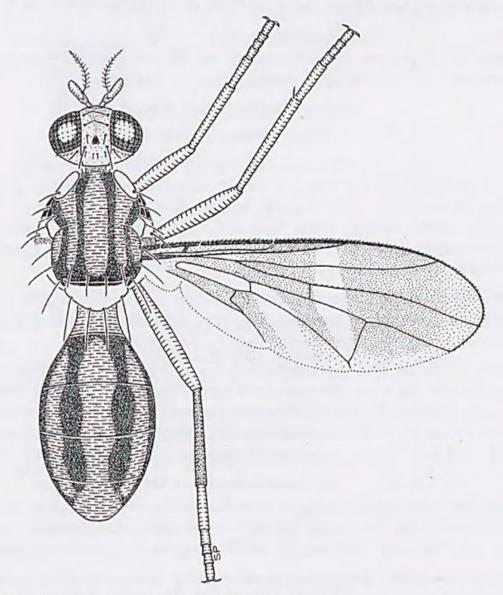


Fig. 2. Parasophira concinna (Walker): male from Sarawak.

Phorelliosoma Hendel, 1914

(= Staurellina Hering, 1941; = Mimosophira Hardy, 1973; = Orienticaelum Ito, 1984).

The limits and synonymy of this genus were discussed by Hancock (2011b), who included six species from East and Southeast Asia.

Species: ambitiosum Hering; femoratum (Shiraki); hexachaeta Hendel (= Mimosophira rubra Hardy) [type species]; hilaratum Hering; parvisetalis (Hering); trypetopsis (Hering).

Proptilona Zia, 1965, stat. rev.

(= Heterosophira Hardy, 1973, syn. n.; = Spaniothrix Hardy, 1973, syn. n.).

Removed from synonymy with *Kambangania* and reinstated as a distinct genus (with two new synonyms, both also removed from *Kambangania*) to include four species from Southeast Asia. *Proptilona* differs from *Kambangania* and related genera in characters noted in the key.

Species: decora (Hardy), comb. n. [ex Kambangania]; uncinata (Hering), comb. n. [ex Acanthonevra Macquart: see Hancock 2011b]; vittata (Hardy), comb. n. [ex Kambangania]; yunnana Zia [type species].

Seraca Walker, 1860, stat. rev.

(= Heringomyia Hardy, 1986; = Emheringia Hardy, 1989).

Placed as a synonym of *Sophira* by Hardy (1980) but informally recognised as a distinct genus by Hancock and Drew (2003). As noted in the key, the wing pattern differs significantly from anything seen in *Sophira* or related genera. Three species from Sulawesi and Ambon are included; other Sulawesian species are referred to *Colobostrella*. For generic synonymy see Hancock and Drew (2003).

Species: kurahashii (Hardy), comb. n. [ex Sophira]; linduensis (Hardy), comb. n. [ex Sophira]; signifera Walker (= Colobostrella heinrichi Hering; = Acanthoneura longiplaga Hering, syn. n.) [type species].

I am unable to find any characters separating *Seraca* (= *Emheringia*, a replacement name for *Heringomyia*) *longiplaga* (Hering) from Ambon and *Seraca signifera* Walker from Sulawesi and consider them synonymous. Weak secondary scutellar setae are also known in *S. kurahashii* (see Hardy 1980) and their relative development appears to be an infraspecific character.

Soosina Hering, 1941

Formerly included as a subgenus of *Sophira* and reinstated as a genus by Korneyev (1999). The wing pattern of the two included species from Java and West Malaysia is distinctive; other characters are noted in the key.

Species: extranea (de Meijere) [type species]; malaysiae (Hancock & Drew) (Fig. 3).

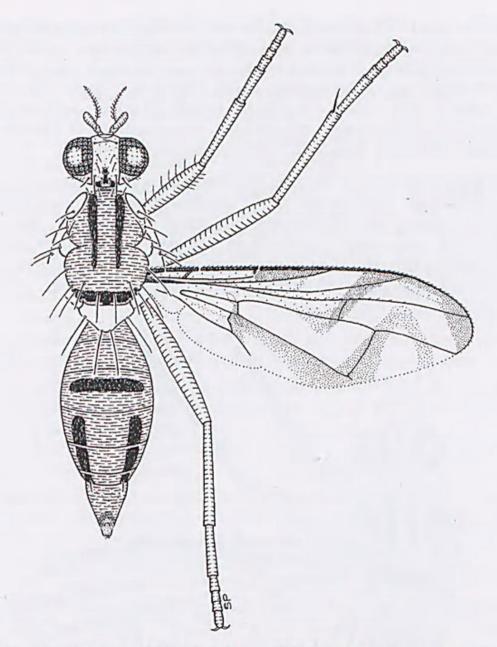


Fig. 3. Soosina malaysiae (Hancock & Drew): holotype female from West Malaysia.

Sophira Walker, 1856

(= Icteroptera van der Wulp, 1899).

Here modified to include 11 species from Sundaland, Mindanao and NE India; others have been referred to different genera.

Species: appendiculata Enderlein; borneensis Hering, stat. n. [raised from subsp. of limbata]; cameronia Hancock & Drew; flavicans (Edwards); flavomaculata (de Meijere); limbata Enderlein; limbipennis (van der Wulp) (= insueta Hering, syn. n.); maculata (van der Wulp); philippinensis Hardy; phlox Munro; venusta Walker [type species] (Fig. 4).

Specimens of S. limbata recorded from Sarawak (Perkins 1938) were referred to S. l. borneensis by Hardy (1980) but true S. limbata was recorded from

Brunei by Chua (2000), suggesting that one variable or two sympatric species are involved. Pending further evidence the latter arrangement is adopted here, particularly since no intermediates have been recorded and infraspecific variation within the genus appears slight. Males of *S. borneensis* have the genae produced and apically 'feathered' (Hardy 1988), a condition not seen in males of *S. philippinensis*; the condition is uncertain for *S. limbata* and *S. limbipennis* since only females of these species are known.

Based on a comparison of their original descriptions and illustrations (van der Wulp 1899 [type lost], Hering 1952), *Sophira insueta* is placed as a new synonym of *Icteroptera limbipennis*. The apical parts of veins R_{4+5} and M appear to be inaccurately portrayed in van der Wulp's figure but other aspects, particularly the broad costal band narrowly overlapping vein R_{2+3} , render them inseparable; both were described from western Java.

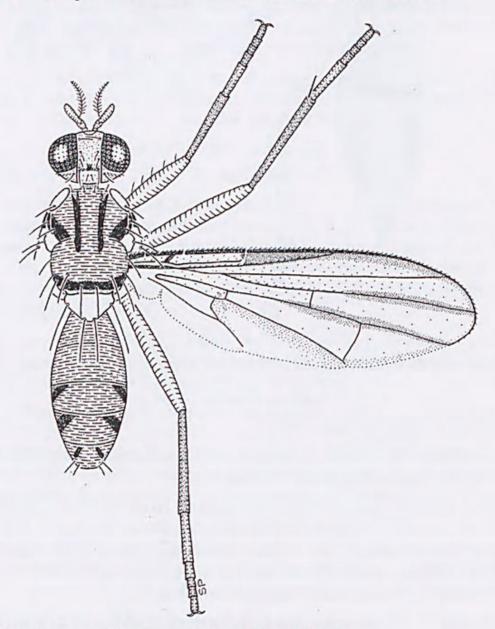


Fig. 4. Sophira venusta Walker: male from West Malaysia.

Ke	ey to genera and species
1	Wing with R-M crossvein placed well beyond middle of cell dm and closer than its own length to DM-Cu crossvein; vein M distinctly curved posteriorly along margin of cell br so that cell dm is hatchet-shaped, much broader apically than basally and medially
-	Not as above; wing cell dm of normal shape, gradually broadening towards apex and not distinctly hatchet-shaped
2	Wing pattern black with large hyaline spots in cells r ₁ , br, r ₄₊₅ and dm and indentations along wing margin in cells m and cu ₁ ; vein R ₂₊₃ sharply curved anteriorly in apical portion to fuse with vein R ₁ and costa; apical portions of veins R ₄₊₅ and M strongly convergent; scutum with 3 narrow black longitudinal vittae [eastern Indonesia (West Papua) and Papua New Guinea; <i>Agnostophana veterrima</i> Hering, 1953 is a synonym]
-	Wing pattern not as above, yellow basally and with a large brown patch or transverse band in outer half; scutum without a dark medial vitta 3
3	Wing with a large, rounded dark patch in outer half; R-M crossvein almost horizontal, on the same line as the apical portion of vein M and running parallel with apical portion of vein R ₄₊₅ ; scutum yellow except for a tiny black spot behind each wing base; secondary scutellar setae vestigial [Solomon Islands] <i>Exallosophira elegans</i> Hardy, 1980
-	Wing with a dark transverse band across R-M and DM-Cu crossveins, separated from dark apical area by a hyaline band across wing; scutum yellow with 2 longitudinal black vittae; secondary scutellar setae well developed [Fiji; illustrated by Malloch 1939b]
4	Wing veins R_{2+3} with 1 or 2 posteriorly-directed spurs or crossveins; vein M with last portion curved anteriorly towards vein R_{4+5} ; vein R_{2+3} distinctly angled anteriorly in apical portion
-	Wing veins R ₂₊₃ without posteriorly-directed spurs or crossveins; if vein M with last portion curved anteriorly then either stigma much longer than cell c or vein M setose above and below
5	Two strong spurs from vein R_{2+3} almost crossing cell r_{2+3} plus one directed towards or connecting with apex of stigma; apical portions of veins R_{4+5} and M strongly convergent; R-M crossvein no more than its own length from DM-Cu crossvein
-	One strong spur from vein R ₂₊₃ and with or without a spur towards stigma; apical portions of veins R ₄₊₅ and M running more or less parallel; R-M crossvein distinctly more than its own length from DM-Cu crossvein; secondary scutellar setae vestigial or absent
6	Secondary scutellar setae normally distinct; intrapostalar setae present

-	Secondary scutellar setae vestigial or absent; intrapostalar setae absent Polyaroidea Hardy 9
7	Wing apex mostly hyaline, mottled with brown; face black between antennae [Papua New Guinea]
_	Wing apex broadly brown; face entirely yellow
8	Wing with a distinct transverse brown band across R-M and DM-Cu crossveins; intrapostalar and secondary scutellar setae weak and hair-like [Papua New Guinea]
-	Wing without a distinct transverse brown band across R-M and DM-Cu crossveins from apex of cell r ₁ ; intrapostalar and secondary scutellar setae well developed [eastern Indonesia (Aru, Misool, West Papua) and Papua New Guinea]
9	Thorax and abdomen largely shiny black; wing with R-M crossvein on line of DM-Cu crossvein and a narrow transverse band from apex of cell bm to wing margin at apex of vein A ₁ +Cu ₂ [Papua New Guinea]
-	Thorax and abdomen yellow to reddish-brown; wing with R-M crossvein slightly before line of DM-Cu crossvein and without a narrow transverse band from apex of cell bm to wing margin
10	Ocellar setae weak; 2 pairs of orbital setae; prescutellar acrostichal setae present; wing cells R ₁ and R ₂₊₃ between spurs with a hyaline indentation [Papua New Guinea]
-	Ocellar setae well developed; 1 pair of orbital setae; prescutellar setae absent; wing cells R_1 and R_{2+3} between spurs without a hyaline indentation [Papua New Guinea] Polyaroidea univittata Hardy, 1988
11	Wing cell c about as long as stigma and both cells brown; wing with broad, brown transverse bands basally and medially and apex broadly brown; frontal, orbital and ocellar setae well developed; thorax and abdomen not densely haired; intrapostalar setae present [Papua New Guinea]
-	Wing cell c distinctly longer than stigma and both cells yellow; wing with narrow, brown transverse bands crossing R-M and DM-Cu crossveins and apex narrowly brown; frontal, orbital and ocellar setae weak; thorax and abdomen densely yellow-haired; intrapostalar setae absent [Sumatra, West Malaysia, Sarawak and Sabah; a record from the Philippines with no locality data (Malloch 1939a) has not been traced and requires confirmation]
12	Stigma elongate, longer than cell c and separated from apex of vein R ₂₊₃ by much less than its own length; vein M strongly curved anteriorly in apical portion towards apex of vein R ₄₊₅ ; secondary scutellar setae vestigial or absent; frontal setae absent [Neosophira Hendel, 1914 is a synonym; genus revised by Hardy 1958a] Terastiomyia Bigot 13

-	Not as above; if vein M strongly curved anteriorly in apical portion towards apex of vein R_{4+5} then vein M setose and stigma not longer than cell c and separated from apex of vein R_{2+3} by much more than its own length
13	Face yellow; abdomen black with a longitudinal, yellow medial vitta; wing cell R ₄₊₅ without hyaline markings beyond line of DM-Cu crossvein [Sula I. east of Sulawesi]
-	Face with a large black medial spot; abdomen not as above; wing cell R ₄₊₅ with a hyaline streak beyond line of DM-Cu crossvein
14	Wing with stigma very elongate, ending at or beyond level of DM-Cu crossvein; costa at apex of cell r ₁ much shorter than in cell r ₂₊₃ ; apical half of wing with longitudinal hyaline streaks; scutum entirely rufous; genae not produced in males [Sulawesi; <i>Enicoptera pictipennis</i> Walker, 1860 is a synonym]
-	Wing with stigma ending well before level of DM-Cu crossvein; costa at apex of cell r ₁ about equal to that in cell r ₂₊₃ ; apical half of wing with a C-shaped hyaline band from apex of vein M to apical part of cell dm; scutum with a large black spot behind each postpronotal lobe; genae produced into lobes in males [Sulawesi and Ambon; <i>Enicoptera arcuosa</i> Walker, 1860 and <i>Neosophira ferruginea</i> . Hendel, 1914 are synonyms]
15	Wing cell bcu elongate with the apex blunt or weakly acute but not produced into a distinct lobe; stigma shorter than cell c; wing pattern reduced to dark patches largely beyond line of R-M crossvein; secondary scutellar setae vestigial or absent; presutural setae absent
-	Wing cell bcu with the apex produced into a distinct lobe; stigma often as long as or longer than cell c; wing pattern variable, often extensive basally; presutural setae present or absent
16	Head with 2 pairs of distinct frontal setae; scutum with 4 black longitudinal vittae, the lateral pair restricted to the postsutural region; wing cells bc, c and stigma not conspicuously slender and stigma less than half length of cell c; middle femora with 2 rows of stout ventral spines [southern (peninsular) Thailand] Adramoides picta Hardy, 1973
-	Head without distinct frontal setae; scutum without longitudinal vittae; wing cells bc, c and stigma conspicuously slender and stigma more than half length of cell c; middle femora without rows of stout ventral spines; postpronotal setae absent
17	All head and body setae absent; scutellum with a pair of distinct subapical tubercles; wing pattern reduced to a small, apical dark patch; R-M crossvein placed well beyond middle of cell dm, about its own length from DM-Cu crossvein [Papua New Guinea; illustrated by Hardy 1983]

- Head and body setae not all absent; scutellum without subapical tubercles; wing with a dark transverse band from costa in cell r₁ to vein M above apical part of cell dm and a large subapical dark patch with a large, round hyaline indentation in cell m; R-M crossvein placed near middle of cell dm [Philippines (Mindanao)] Pseudosophira bakeri Malloch, 1939

- 19 Vein M not strongly curved anteriorly in apical portion towards apex of vein R₄₊₅; anterior notopleural seta enclosed in a black lateral patch; wing with broad transverse brown bands from costa at end of cell c to behind base of vein R₄₊₅ and from apical half of stigma across RM crossvein to middle of cell dm, plus a broad apical area from line of DM-Cu crossvein enclosing a hyaline patch across vein M in cells r₄₊₅ and m [Thailand, West Malaysia (Fig. 5)] Langatia setinerva Hancock & Drew, 1995

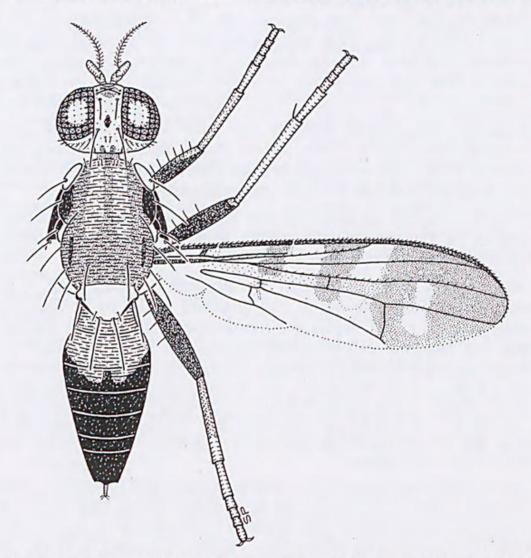


Fig. 5. Langatia setinerva Hancock & Drew: holotype female from West Malaysia.

- 20 Wing dark brown except for a narrow hyaline posterior margin; scutum with a white, elongate medial vitta extending onto scutellum; abdomen entirely black [India, Burma, Thailand, Laos, S China (Guangxi: Wang and Chen 2002), West Malaysia; illustrated by Hancock and Drew 1994 and Dohm et al. 2008] Felderimyia fuscipennis Hendel, 1914
- 21 Scutum entirely pale; wing with cell br mostly hyaline and an oval hyaline spot at base of cell r₄₊₅ between R-M and DM-Cu crossveins; abdominal terga 1-2 with black sublateral bands, 3 entirely pale and 4-5 black [Laos, West Malaysia; illustrated by Dohm *et al.* 2008 (Fig. 6)]

 Felderimyia flavipennis Hancock & Drew, 1994

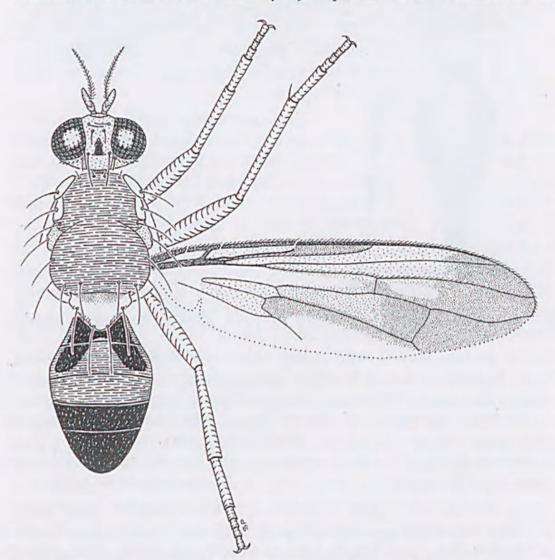


Fig. 6. Felderimyia flavipennis Hancock & Drew: holotype male from West Malaysia.

Scutum with black lateral presutural patches and broad, dark dorsolateral postsutural vittae; wing with cells br and base of r₄₊₅ pale brown; abdomen black except pale medially on terga 2-5 [S China (Yunnan: Dohm et al. 2008), Thailand, West Malaysia; illustrated by Dohm et al. 2008 (Fig. 7)] Felderimyia gombakensis Hancock & Drew, 1995

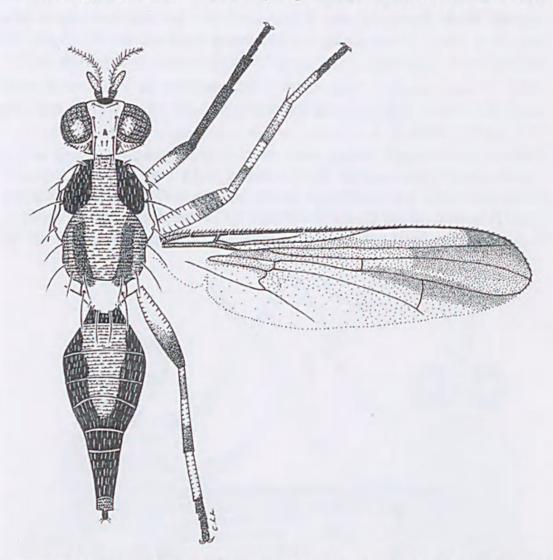


Fig. 7. Felderimyia gombakensis Hancock & Drew: holotype female from Malaysia.

- Wing pattern often reduced but not with a transverse basal and two oblique discal bands; stigma often as long as or longer than cell c; head normally with 1 or 2 pairs each of frontal and orbital setae, the upper orbitals often reduced; scutum often with dark submedian vittae 27

23	Scutum yellow with a black lateral presutural spot and lateral postsutural streak; abdominal terga 3-5 each with a pair of black spots; face entirely yellow [Taiwan; illustrated by Hardy 1958b]
-	Scutum with the black postsutural vittae broad and either L- or C-shaped; face black or yellow
24	Scutum with dark lateral vittae straight-sided or almost L-shaped 25
_	Scutum with dark vittae C-shaped, curving inwards at either end 26
25	Face with a large black medial spot; scutum with a pale brown spot on the inner side of each lateral vitta; abdomen with black basolateral patches on terga 3-5 (in female) or 4-5 (in male); [Sri Lanka; illustrated by Senior-White 1922] <i>Tritaeniopteron punctatipleurum</i> (Senior-White, 1922)
_	Face entirely yellow; scutum with a pair of black submedial vittae extending posteriorly to level of supraalar setae; abdomen with black transverse basal bands across terga 3-5 and lateral margins of terga 2-4 broadly black; scutum with dark lateral vittae connected along posterior margin [Philippines (Luzon)] <i>Tritaeniopteron flavifacies</i> Hardy, 1974
26	Face with a large black medial spot; abdomen with transverse black basal bands on terga 3-5 [Indonesia (Java); illustrated by Hardy 1958b] Tritaeniopteron eberneum de Meijere, 1914
-	Face entirely yellow; abdominal terga 3-5 with black basolateral marks extending basally towards mid-line and often separated into an additional pair of submedian spots [northern, central and southern Thailand; black markings on scutum and abdomen a little variable in extent; illustrated by Hancock and Drew 1994, who placed <i>T. elachispilotum</i> Hardy, 1973 as a synonym]
27	Wing with stigma normally about half to two-thirds length of cell c; cell c entirely hyaline; cell r_{4+5} with a hyaline spot or indentation with its midline just beyond line of DM-Cu crossvein or pattern reduced and cell r_{4+5} entirely hyaline above DM-Cu crossvein; cell cu ₁ largely hyaline, at least basally and medially; presutural setae usually absent; secondary scutellar setae often distinct
	Wing usually with stigma almost as long as to longer than length of cell c; if distinctly shorter then with a hyaline indentation from costa at apex of stigma that encloses R-M crossvein; cell c often at least partly coloured; cell r_{4+5} usually without a hyaline spot or indentation just beyond line of DM-Cu crossvein; head normally with 1 pair of distinct frontal setae, sometimes with a weak second pair anteriorly; presutural setae usually present; secondary scutellar setae normally very weak or absent 37
28	Arista pubescent; 2 pairs of distinct frontal setae; 2 pairs of orbital setae situated on upper part of head, the upper orbital seta often weak; wing distinctly narrow, with cell cu ₁ almost entirely hyaline and pattern often

	reduced to isolated patches; secondary scutellar setae distinct, a third to a half length of apicals
_	Arista plumose; 1 pair of distinct frontal setae and sometimes a weak anterior pair; 1 pair of distinct lower orbital setae situated near middle of frons, the upper pair of orbital setae usually weak or absent; wing no distinctly narrow and cell cu ₁ not almost entirely hyaline; scutum with 4 dark longitudinal vittae, usually united posteriorly; apex of cell r ₂₊₃ ofter subhyaline, basal and apical dark patches separated by a broad hyaline indentation from costa in cell r ₁ to vein Cu ₁ at apex of cell dm and the large hyaline spot in cell r ₄₊₅ adjacent to line of DM-Cu crossvein united or almost united with a broad hyaline indentation in cell m; secondary scutellar setae very weak or absent
29	Scutum with 4 dark longitudinal vittae; wing pattern extensive, extending broadly into anterior half of cell dm; cell r ₁ with a broad, triangular hyaline indentation beyond apex of stigma
-	Scutum with no or 2 dark longitudinal vittae; wing pattern reduced to isolated patches medially, apically and along DM-Cu crossvein; cell r with a broad, rectangular hyaline indentation extending across wing 31
30	Prescutellar acrostichal setae present [China (Hubei, Fujian, Sichuan Guangxi)]
-	Prescutellar acrostichal setae absent [Japan (Honshu, Shikoku)]
31	Wing with medial dark patch behind stigma extending broadly to vein M in apical half of cell br and enclosing a hyaline spot posteriorly 32
-	Wing with medial dark patch behind stigma reduced to separated spots in cell r ₁ and across R-M crossvein and not enclosing a hyaline spot in cell br
32	Scutellum normally with a pair of dark spots; wing with pattern extending weakly into cell dm behind R-M crossvein and halfway into cell r ₄₊₅ before DM-Cu crossvein; stigma entirely dark [Taiwan, Vietnam; <i>Mimosophira rubra</i> Hardy, 1973 was placed as a synonym by Wang (1998); records from NE Burma and SW China (Wang 1998) belong to <i>P. hilaratum</i>]
-	Scutellum without a pair of dark spots; wing with pattern extending no more than very faintly into cell dm behind R-M crossvein or into cell r ₄₊₅ before DM-Cu crossvein; stigma often paler at base [NE Burma and SW China (SE Xizang [Tibet]); illustrated by Wang 1998, as 'P. hexachaeta']
33	Wing with apical dark patch entire from apex of cell r ₁ to beyond apex of vein M in cell m, the apical part of cell r ₂₊₃ dark except for a small hyaline central spot [NE India; illustrated by Hering 1941b]
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-	Wing with apical dark patch reduced to isolated patches from apex of cell r ₁ and at wing apex, separated by a broad hyaline area in cell r ₂₊₃ [NE Burma; illustrated by Hering 1941a, as <i>Staurellina trypetopsis</i>]
34	Wing with broad hyaline indentation in cell m extending anteriorly across cell r ₄₊₅ into cell r ₂₊₃ and curving towards wing apex behind vein R ₂₊₃ ; abdomen largely reddish-yellow, tinged with black on lateral margins [central Burma; illustrated by Hering 1938, as <i>Pseudacidia uncinata</i>] **Proptilona uncinata* (Hering, 1938)
-	Wing with broad hyaline indentation in cell m usually extending across cell r_{4+5} but not crossing vein R_{4+5} into cell r_{2+3}
35	Scutum with vittae not connected posteriorly; abdomen reddish-brown, paler medially [S China (Yunnan)] Proptilona yunnana Zia, 1965
-	Scutum with submedial pair or all 4 vittae connected by a black band along posterior margin
36	Wing with hyaline spot in cell r ₄₊₅ narrowly separated from indentation in cell m along vein M; dorsocentral setae absent; abdomen black with a yellow medial vitta [C & S Thailand] Proptilona decora (Hardy, 1973)
-	Wing with hyaline spot in cell r ₄₊₅ broadly united with indentation in cell m across vein M; dorsocentral setae present; abdomen largely brownish-red to black [N & C Thailand, Laos] <i>Proptilona vittata</i> (Hardy, 1973)
31	Wing with a hyaline indentation from costa at apex of stigma extending to and enclosing R-M crossvein; presutural setae present
-	Wing with hyaline indentation from costa at apex of stigma absent or not enclosing R-M crossvein but crossing base of cell r ₄₊₅ into cell dm 46
31	Wing with three broad, posterior hyaline indentations, 1 from apex of cell m across vein M into cell r ₄₊₅ , 1 in cell m alongside DM-Cu crossvein and 1 obliquely across basal part of cell cu ₁ into base of cell dm; stigma short, about half length of cell c; eyes broadly protuberant in both sexes; face concave in profile; scutum with posterior half black and anterior half yellow with a dark transverse band level with anterior notopleural and presutural setae [Sabah] Homoiothemara eurycephala Hardy, 1988
-	Not as above; wing with a transverse hyaline band in apical half of cell dm that normally curves anteriorly into cell r_{4+5} and sometimes forms a complete or interrupted inverted C- or U-shaped band extending across cell r_{2+3} to apices of cells r_{4+5} or m; stigma distinctly longer than half length of cell c; face vertical in profile or slightly concave near epistomal margin; scutum without a dark transverse band anteriorly
3	Wing with stigma distinctly shorter than cell c and with a large rounded dark patch in distal half separated from a narrow dark costal band and united transverse band by a hyaline C-shaped band from middle part of cell dm to apex of cell r ₄₊₅ and with a parallel hyaline band behind its

- apical part to apex of vein M; head broad; scutum without dark submedial vittae [N and C Sulawesi] Cleitamiphanes heinrichi Hering, 1941

- Basal half of wing without hyaline indentations; DM-Cu crossvein not strongly bowed, the posterior half distinctly divergent from wing margin; scutum black or with 4 black spots, the posterior pair often extended anteriorly as short vittae extending to or beyond supraalar setae; secondary scutellar setae weakly present Colobostrella Hendel ... 43
- 41 Abdominal terga 1-4 yellow medially and black laterally, tergum 5 mostly or entirely black; wing pattern variable, the hyaline band from apical part of cell dm reaching or just crossing vein R₄₊₅ anteriorly, or joined with hyaline indentation from cell m by a loop through cell r₂₊₃ [Sulawesi and Ambon; *Acanthoneura longiplaga* Hering, 1939 and *Colobostrella heinrichi* Hering, 1942 are synonyms] *Seraca signifera* Walker, 1860
- At least abdominal terga 3-4 with broad transverse dark basal bands ... 42

- Wing cells m and r₄₊₅ beyond R-M crossvein without hyaline indentations and band from cell dm ending as a curved hook in cell r₂₊₃; scutum with 4 black spots, the posterior pair extended anteriorly as short vittae 45

-	Head and face yellow; scutum pale with 4 black spots; wing with the
	hyaline band continuing through apical part of cells r ₂₊₃ and r ₄₊₅ to
	extreme apex of cell m; abdomen almost entirely pale [C Sulawesi]

- Face vertical in profile or slightly concave near epistomal margin; scutum with at most 2 longitudinal vittae and a lateral patch between postpronotal lobe and suture that normally connects with a dark band over an episternum; wing pattern not as above, if with a broad, transverse hyaline band between RM and DM-Cu crossveins to apex of cell dm then wing pattern largely yellow and abdomen with arcuate basal black bands across terga 2-4; cell cu₁ usually with a dark anterior band along vein Cu₁ behind cell dm that often continues as a dark band over DM-Cu crossvein

- 48 Scutum with 2 black vittae, the lateral pair discontinuous or forming a patch united with anepisternal band; abdomen with black arcuate bands across bases of terga 2 and 3 and broadly black laterally on terga 4-6 [Sarawak, Sabah, Kalimantan] ... Kambangania simillima (Hering, 1952)
- 49 Scutum with submedial vittae connected posteriorly; scutellum entirely yellow; wing cell m without a hyaline indentation; dark discal area broadly diffuse around entire apical margin; mid basitarsus of male with a medial concavity; abdomen with arcuate black bands across bases of terga 2 and 3 and terga 3-6 broadly black laterally and yellow medially [Sumatra, West Malaysia, Sarawak; Sophira (Kambangania) disjuncta Hardy, 1980 is a synonym (Fig. 8)]

...... Kambangania ypsilon (Rondani, 1875)

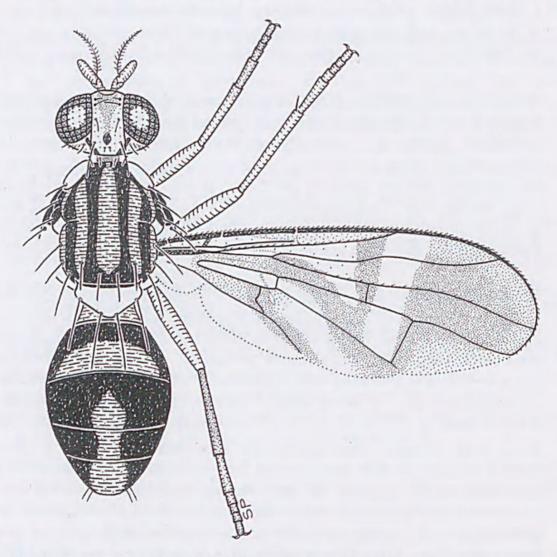


Fig. 8. Kambangania ypsilon (Rondani): male from West Malaysia.

- 51 Wing pattern with two sinuous, yellow to brown bands, one from anteromedial part of cell dm across R-M crossvein to apical part of cell r₁ and along costa to apex of cell r₄₊₅, the other from base of cell cu₁ along posterior margin of vein Cu₁ and across DM-Cu crossvein, forming an inverted U-shaped band in cell r₄₊₅ and crossing vein M to wing margin in cell m; R-M crossvein placed within apical third of cell dm and beyond apex of stigma; head with upper pair of orbital setae distinct; scutum with 2 longitudinal black vittae that end well before the black band along posterior margin and no lateral black patch or band between postpronotal lobe and suture; scutellum with only a few fine hairs on disc; abdomen with an isolated pair of black sublateral bands on terga 3-6 or 4-6

- Not as above; wing with distinct dark areas and scutum with the 2 submedial longitudinal black vittae complete or almost complete 57

- 57 Wing with anterior margin dark brown from apex of vein Sc to or beyond apex of vein R₂₊₃ and with a broad, dark longitudinal band through upper part of cell cu₁ along vein Cu₁, across apical part of cell dm and DM-Cu crossvein and along lower part of cell r₄₊₅ along vein M to wing apex; abdominal bands on terga 2-4 sometimes conspicuously reduced 58

- Wing with dark costal band narrow, not reaching or extending behind vein R₂₊₃; margin entirely pale from apex of vein R₂₊₃ to beyond apex of vein R₄₊₅; an episternum with a broad black vertical band60

- Wings largely dull brown with diffuse anterior and apical margins, a triangular hyaline patch in apical half of cell br and most of cell dm and hyaline posterior margin filling most of cell cu₁ behind a dark band along vein Cu₁; male without a distinct lobe to cell cu₁ at apex of vein A₁+Cu₂ [West Malaysia (Fig. 9)] Sophira cameronia Hancock & Drew, 1995

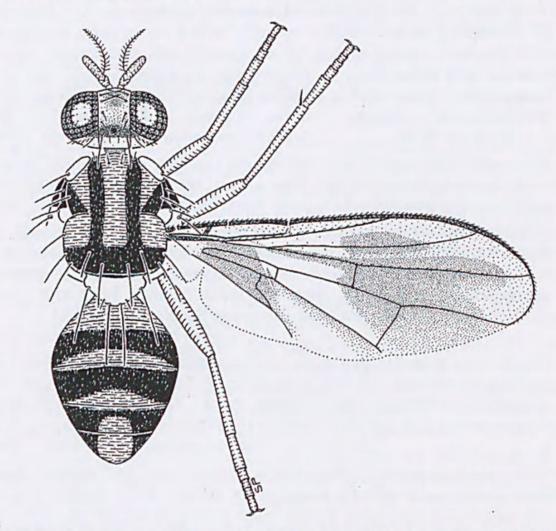


Fig. 9. Sophira cameronia Hancock & Drew: holotype male from West Malaysia.

* An undescribed species from Sabah (Hardy 1988: 113) keys here but differs from the remaining species in wing pattern, particularly the narrow brown band running along veins Cu₁ and DM-Cu and looping over the apical portion of vein M to end at the wing margin in the upper part of cell m.

Discussion

The large number of monotypic genera reflects the distinctive nature of many of the species in this complex. It is likely that further study will enable some of these to be synonymised and combined, but at present there is insufficient evidence to establish this. Presutural setae are present in some species (e.g. Felderimyia flavipennis, Proptilona uncinata) in genera where they otherwise do not occur and this character is possibly subject to reversal.

The New Guinea genera *Polyara*, *Polyaroidea* and *Pseudacrotoxa* were previously referred to an unplaced group possibly allied to the Phascini (Korneyev 1999, Hancock and Drew 2003), based largely on the vanes of the phallapodeme being fused into a Y-shaped structure; however, this state occurs in a number of different lineages within subfamily Phytalmiinae (including *Rioxa* Walker) (Korneyev 1999) and appears to be homoplasious. The rearing of this group of genera from the stems of living bamboo (Hardy 1986, 1988) supports their association with the *Sophira* complex.

This complex is well developed in Sundaland. Several genera are endemic to this region plus the southern Philippine island of Mindanao and there are small radiations of endemic genera into Sulawesi and the Papuan Region. Apart from records of *Sophira venusta* from southern peninsular Thailand (Hancock and Drew 1995b) and *S. philippinensis* from Negros (Hardy 1974), only a single species of these otherwise endemic genera, *Sophira phlox* from NE India, is known outside Sundaland or Mindanao. Similarly, the only two species recorded from Ambon (*Terastiomyia lobifera* and *Seraca signifera*), in the southern Moluccas, also occur in Sulawesi.

The distribution of *Sophira phlox* is unusual, known only from the Garo Hills of western Meghalaya, just north of Bangladesh (Munro 1935). It appears to be derived from the Sumatran *Sophira flavicans*, suggesting a dispersal route via the Nicobar-Andaman islands and western Burma rather than via Southeast Asia proper, where the genus has not been recorded. The latter route is evident in the only other species known from India, the widespread *Felderimyia fuscipennis* and the endemic *Phorelliosoma ambitiosum* from the Himalayan foothills of West Bengal.

Four genera (*Phorelliosoma*, *Proptilona*, *Tritaeniopteron* and *Adramoides*), united by an elongate wing cell c in association with a relatively short stigma, are exclusively or almost exclusively East and Southeast Asian in distribution (an endemic species of *Tritaeniopteron* is known from Java). *Felderimyia* and *Langatia*, with both wing cell c and the stigma elongate, contain four species recorded from both Southeast Asia and West Malaysia; three further species (*Tritaeniopteron tetraspilotum*, *Proptilona decora* and *Adramoides picta*) are known from the southern part of peninsular Thailand and are likely to occur also in West Malaysia. Only a single species, the endemic *Tritaeniopteron punctatipleurum*, is known from Sri Lanka; like *T. eberneum* from Java and *T. flavifacies* from Luzon, it appears to be either an outlier or

isolated relict. Interestingly, the genus *Tritaeniopteron* has not been reported from India.

Three Sulawesian genera, Cleitamiphanes, Colobostrella and Seraca are clearly closely allied and probably synonymous, a possibility also noted for Cleitamiphanes and Colobostrella [as Sophira s.s.] by Korneyev (1999). However, they are maintained as separate genera here pending a better understanding of their relationships, both among themselves and with Homoiothemara and other Sundaland genera in the Sophira complex.

The Acanthonevra group of genera, sensu Korneyev (1999), appears to be divisible into four generic complexes rather than two distinctive subgroups: (1), the Acanthonevra complex as discussed by Hancock (2011b); (2), the Sophira complex discussed here; (3), the Rioxa complex, which includes at least one species [Rioxa discalis (Walker)] collected at cut shoots of bamboo (Permkam 1995) although its status as a host is unconfirmed; and (4), the Dacopsis complex, a group of primarily Australian and New Guinea genera that is known to breed beneath the bark of newly fallen trees, a niche shared with members of the tribe Phytalmiini.

The Sri Lankan genus *Sophiroides* Hendel (with its sole species *S. flammosus* Hendel) is referred to the *Rioxa* complex, together with *Cribrorioxa* Hering, *Ectopomyia* Hardy, *Hexacinia* Hendel, *Hexamela* Zia and *Rioxa* Walker.

The *Dacopsis* complex includes the genera *Austronevra* Permkam & Hancock, *Austrorioxa* Permkam & Hancock, *Copiolepis* Enderlein, *Dacopsis* Hering and *Stymbara* Walker. Several other Australian, New Guinea and Pacific genera included in the *Acanthonevra* group by Korneyev (1999) and Hancock and Drew (2003) appear to belong in the *Dirioxa* group, to which are referred *Anchiacanthonevra* Hardy, *Dirioxa* Hendel, *Griphomyia* Hardy, *Lumirioxa* Permkam & Hancock, *Micronevrina* Permkam & Hancock, *Mimoeuphranta* Hardy and *Parachlaena* Hering. As in the case of the apparently related *Themaroides* group, known larval habitats of the *Dirioxa* group include beneath the rotting bark of standing trees or in various fruits and these two groups are possibly more closely related to *Diarrhegma* Bezzi from Southeast Asia and the *Aethiothemara* group of genera from Africa than to the *Acanthonevra* group as currently recognised.

The New Guinea genus *Gressittidium* Hardy was transferred from the *Acanthonevra* group to the tribe Phascini by Hancock (2011c).

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