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Two new species and a new combination of *Allacta* (Blattodea, Ectobiidae, Pseudophyllodromiinae) from China, with notes on their behavior in nature

Jia-Jun He[1], Yu-Hong Zheng[1], Lu Qiu[1], Yan-Li Che[1], Zong-Qing Wang[1]

1 *Institute of Entomology, College of Plant Protection, Southwest University, Beibei, Chongqing, 400716, China*

Corresponding author: *Zong-Qing Wang* (zqwang2006@126.com)

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Abstract

Two new species, *Allacta bruna* **sp. n.** and *Allacta alba* **sp. n.**, from China are described and illustrated. *Allacta hainanensis* (Liu et al., 2017), **comb. n.** is proposed and re-described; figures including genitalia are provided. A key is provided to all species from China based on males. Notes on the bionomics of this genus in China are provided.

Keywords

Dictyoptera, Blattaria, *Temnopteryx*, cockroaches

Introduction

The genus *Allacta* is widely distributed from southwestern China to northeastern Australia. It consists of 41 known species worldwide, five of which were known from China before this study. Wang et al. (2014) described the species *Allacta xizangensis,* re-described four other known species from China, and distinguished *Allacta* from related genera.

Liu et al. (2017) described a species *Temnopteryx hainanensis* from Hainan, China, based on morphological characters (without providing male genital characters), and which has reduced tegmina and wings. However, Princis (1963) proposed *Temnopteryx* is endemic to South Africa. Princis also established the generic diagnosis as follows:

tegmina absent or shortened, hind wing reduced to lateral lobes or absent; tarsal claws symmetrical and unspecialized; and abdominal terga unspecialized. Fortunately, we obtained specimens of *T. hainanensis* from Hainan Province as well as a photograph of the holotype. We also collected specimens from Zhejiang and Hainan, among which two new species of *Allacta* were discovered, and we use this opportunity to describe them together. With an increase in field surveys, it has been possible to better observe the behavior in nature of *Allacta* species and the members of this genus are commonly found to be tree climbers in the forests.

Materials and methods

Terminology used mainly follows Roth (2003). Genitalia terms are according to McKittrick (1964). Venation terms follow Li et al. (2018). Vein abbreviations in this article are as follows:

CuA	cubitus anterior	**RP**	radius posterior
CuP	cubitus posterior	**ScP**	subcosta posterior
M	media	**V**	vannal
R	radius	**Pcu**	postcubitus
RA	radius anterior		

Measurements are based on specimens examined. The genital segments of the examined specimens were soaked in 10% NaOH and rinsed with distilled water, then stored in glycerin for observation. Genitalia were observed in glycerin using a MOTIC K400 stereomicroscope and genital photographs were taken using an LAS V4.9. Specimen photographs were taken using a Canon 50D plus a Canon EF 100mm f/2.8L IS USM MACRO lens and photos were stacked using Helicon Focus software. All photos were modified in Adobe Photoshop CS6. The materials examined are deposited in the Institute of Entomology, Southwest University, Chongqing (**SWU**) and the Shanghai Entomological Museum, the Chinese Academy of Sciences, Shanghai (**SHEM**).

Taxonomy

Allacta Saussure & Zehntner, 1895

Allacta Saussure & Zehntner, 1895: 45 (New name for *Abrodiaeta* Brunner von Wattenwyl, 1893). Type species: *Abrodiaeta modesta* Brunner von Wattenwyl, 1893, by selection; Roth 1991: 996; Roth 1993: 361; Roth 1995: 51; Roth 1996: 235; Wang et al. 2014: 440.

Arublatta Bruijning, 1947: 224. Type species: *Blatta punctata* Walker, 1869. Synonymized by Roth 1991: 996.

Pseudochorisoblatta Bruijning, 1948: 90. Type species: *Phyllodromia interrupta* Hanitsch, 1925, by selection. Synonymized by Princis 1965: 151.
Euhanitschia Princis, 1950: 178. Type species: *Phyllodromia diagrammatica* Hanitsch, 1923. Synonymized by Roth 1996: 235.
Compsosilpha Princis, 1950: 180. Type species: *Chorisoblatta karnyi* Hanitsch, 1928. Synonymized by Roth 1996: 235.

Diagnosis. Body pale brown to blackish brown, mostly yellowish brown. Clypeus normal, not thickened. Pronotum usually oval, wider than length. Tegmina and wings usually fully developed, a few slightly reduced (*T. hainanensis*). Tegmina with M, CuA oblique, hind wings with R straight, sometimes forked, M and CuA usually straight or nearly so, latter with 1–6 (usually 4 or 5) complete branches; apical triangle small, reduced or absent. Anteroventral margin of front femur Type B_2 or B_3; pulvilli present only on the fourth tarsomere of all legs, tarsal claws symmetrical and unspecialized, arolia present. Male abdominal terga unspecialized. Male genitalia usually have three principal phallomere sclerites, the hook-like phallomere on right side, the median, and the left; most species have an accessory median phallomere. Ootheca not rotated prior to deposition.

Note. Roth (1996) and Wang et al. (2014) discussed the difference among *Allacta*, *Sundablatta,* and *Pseudophyllodromia*, but actually, *Allacta* is closely related with the three genera *Margattea*, *Balta*, and *Sorineuchora* according to Wang et al. (2017), which are also under the subfamily Pseudophyllodromiinae. The most striking difference between *Allacta* and its closely related genera is pulvilli only present on the fourth tarsomere of all legs; or anteroventral margin of front femur Type B_2 or B_3. It is possible that *Allacta* and *Balta* prove to be synonym in the future by molecular method.

Remarks. Roth (1993) erected three species groups under *Allacta* based on color patterns and male interstylar margin, viz. *funebris* species group, *hamifera* species group, and *polygrapha* species group. According to Roth (1993), these three species can be put in the *hamifera* species group, *A. bruna* sp. n. by having a dark pronotum and keel-like ridge at interstylar margin (Figs 4, 11) and *A. alba* sp. n. and *A. hainanensis* (Liu et al. 2017) comb. n. by the two close lobes between the styli (Figs 23, 34).

Checklist of *Allacta* species from China

Allacta bimaculata Bey-Bienko, 1969: 858. China (Yunnan, Guangxi)
Allacta ornata Bey-Bienko, 1969: 859. China (Yunnan, Hainan)
Allacta robusta Bey-Bienko, 1969: 860. China (Yunnan)
Allacta transversa Bey-Bienko, 1969: 859. China (Hainan); Vietnam
Allacta xizangensis Wang et al., 2014: 449. China (Xizang)
Allacta alba sp. n. China (Zhejiang)
Allacta bruna sp. n. China (Hainan)
Allacta hainanensis (Liu et al., 2017), comb. n. China (Hainan)

Key to species of *Allacta* from China (males)

1 Tegmina and wings reduced, not reaching the end of the abdomen ..... ***A. hainanensis* (Liu et al., 2017), comb. n.**
– Tegmina and hind wings fully developed, both extending beyond end of abdomen **2**
2 Pronotal disc with trapezoidal symmetrical white maculae ..... ***A. alba* sp. n.**
– Pronotal disc without white maculae **3**
3 Interocular space with pale brown horizontal stripe **4**
– Interocular space without pale brown horizontal stripe **5**
4 Disc of pronotum totally blackish brown, subgenital plate asymmetrical ..... ***A. bimaculata***
– Disc of pronotum with irregular maculae, subgenital plate symmetrical..... ***A. transversa***
5 Pronotum brown without maculae ..... ***A. bruna* sp. n.**
– Pronotum with maculae..... **6**
6 Head with 2 dark brown longitudinal stripes reaching from the vertex to the frons between the antennal sockets, and subgenital plate with dissimilar styli .... ***A. robusta***
– Head with 1 dark brown longitudinal stripe reaching from the vertex to the clypeus or not, and subgenital plate with similar styli..... **7**
7 Subgenital plate symmetrical, hind margin of subgenital plate nearly straight in the middle ..... ***A. ornata***
– Subgenital plate asymmetrical, hind margin of subgenital plate concave in the middle ..... ***A. xizangensis***

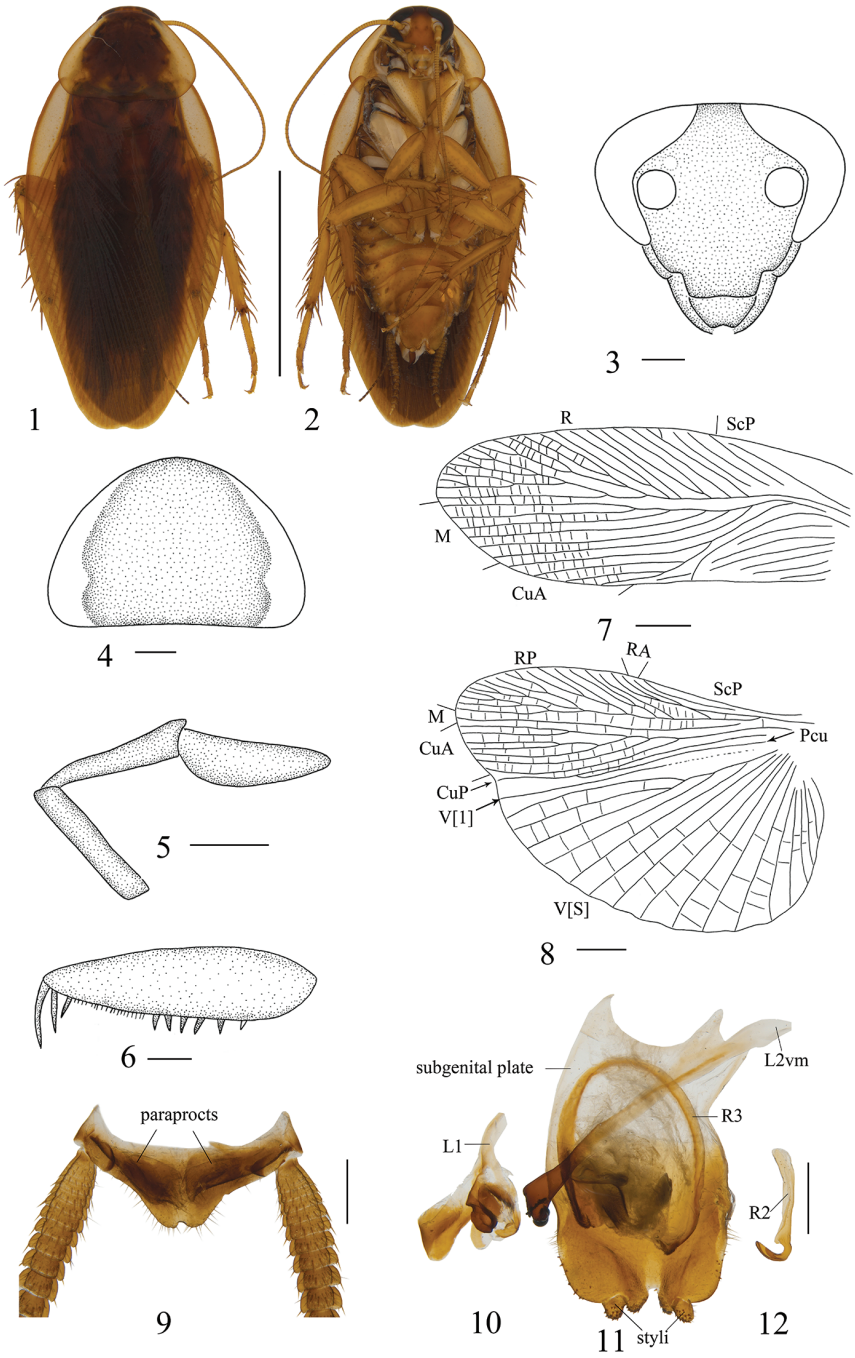
***Allacta bruna* sp. n.**
http://zoobank.org/04466EA4-A061-436E-8872-6E50F80A2560
Figs 1–12, 46

Type material. ***Holotype:*** male, CHINA, Hainan Province, Jianfengling, Mingfenggu, 960 m, 26-V-2014, Shun-Hua Gui, Xin-Ran Li et Jian-Yue Qiu leg. ***Paratypes:*** CHINA, Hainan Province: 1 male, same data as holotype; 1 male, Limushan, 678–694 m, 17-IV-2015, Xin-Ran Li et Zhi-Wei Qiu leg.; 2 females, Jianfengling, Mingfenggu, 26-IV-2015, Lu Qiu et Qi-Kun Bai leg.; 1 female, Diaoluoshan, 17-IV-2015, Lu Qiu et Qi-Kun Bai leg. (all in SWU).

Diagnosis. This species can be easily distinguished from its congeners by the brownish body that lacks any markings.

Measurements (mm). Male, pronotum: length × width 4.5 × 6.8, tegmina length: 15.5, overall length: 18.9–19.2; female, pronotum: length × width 4.7 × 6.7–6.8, tegmina length: 14.1–14.3, overall length: 18.1–18.3.

Description. ***Male.*** Body brown to dark brown (Figs 1, 2). Head brown. Ocelli spots white. Antennae yellowish brown. Frons brown and clypeus pale brown. Maxil-



Figures 1–12. *Allacta bruna* sp. n., male. **1** paratype, dorsal view **2** paratype, ventral view **3** head, ventral view **4** pronotum, dorsal view **5** maxillary palpi segments 3–5, ventral view **6** front femur, ventral view **7** tegmen, dorsal view **8** hind wing, dorsal view **9–12** holotype **9** supra-anal plate and paraprocts, dorsal view **10** left phallomere, dorsal view **11** subgenital plate and median phallomere, dorsal view **12** hook-like phallomere, dorsal view. Scale bars: 1.0 cm (**1, 2**), 0.5 mm (**3–8**), 1.0 mm (**9–12**).

lary palpi pale yellowish brown (Fig. 2). Pronotal disc dark brown, and two lateral borders yellowish brown (Figs 1, 4). Tegmina, wings, and legs brown (Figs 1, 2). Abdomen pale yellowish brown. Cerci black brown (Fig. 2).

Vertex with interocular space about half the distance between antennal sockets (Fig. 3). The third, fourth and fifth maxillary palpi of approximately same length (Fig. 5). Pronotum nearly trapezoidal, broader than long, maximum width behind the middle, the front and hind margins nearly straight, and the postero-lateral angle blunt and round (Fig. 4). Tegmina and wings fully developed, both extending beyond the end of abdomen. Tegmina with M and CuA longitudinal (Fig. 7). Hind wings with M straight and simple; CuA slightly curved with 4 branches (Fig. 8). Anteroventral margin of front femur type B_2 (Fig. 6). Pulvilli only present on the fourth tarsomere. Tarsal claws symmetrical and unspecialized, arolium present. The first tarsus of the front legs about equal in length to the sum of the other four, but obviously longer in the middle and hind legs.

Female similar to the male. The coloration of living individuals dark brown, dried specimens much lighter, especially in the legs. Margins of pronotum and tegmina subtransparent in the specimens.

Male abdomen and genitalia. Abdominal terga unspecialized. Supra-anal plate nearly triangular, and the hind margin obviously concave. Paraprocts simple (Fig. 9). Subgenital plate nearly symmetrical, the middle part of the hind margin has a V-shaped concavity; styli similar, short cylindrical, with small spines, and interstylar margin with two lobes (Fig. 11). Left phallomere complex, inverted Y-shaped (Fig. 10). Median phallomere stem club-like, apex shoe-shaped, base with a small spine, the accessory structure curved, apex brush-shaped (Fig. 11). Hook on the right side (Fig. 12).

Remarks. It can be distinguished from the other species in the group by the tegmina that without any light-colored bar in the anal field.

Etymology. From the Latin word *brunus* referring to the body color being brown without any special markings.

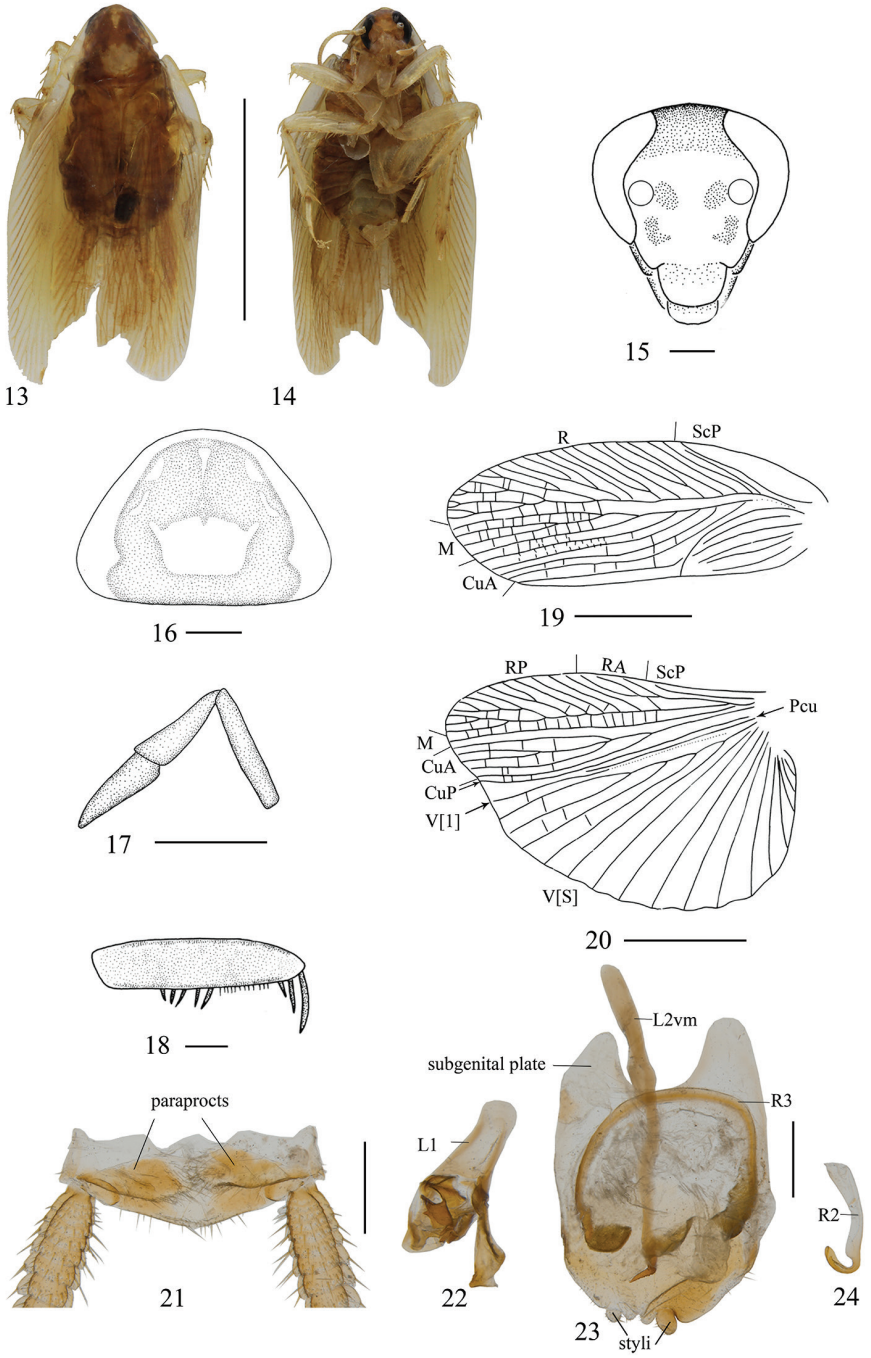
Distribution. China (Hainan).

Allacta alba sp. n.

http://zoobank.org/290F2E8F-1E9D-42F0-9668-B18F9DA9A327
Figs 13–24

Type material. ***Holotype:*** male, CHINA, Zhejiang Province, Longtangshan, Qingliangfeng, 960 m, 6-VIII-2011, Jin-Jin Wang leg. ***Paratype:*** 1 male, same data as holotype (all in SWU).

Diagnosis. This species resembles *A. xizangensis* by the brownish tegmina, which are without distinct strips and spots (Figs 13, 14, 44), and the two small lobes between the styli, but it can be differentiated from the latter by the following characters: 1) pronotum without dark brown strip-like markings, while with dark brown strip-like markings in *A. xizangensis*; 2) two styli unequal in size, while styli similar in *A. xizangensis*; 3) median phallomere with basal part tapering, while in the latter, blunt



Figures 13–24. *Allacta alba* sp. n., male. **13** paratype, dorsal view **14** paratype, ventral view **15** head, ventral view **16** pronotum, dorsal view **17** maxillary palpi segments 3–5, ventral view **18** front femur, ventral view **19** tegmen, dorsal view **20** hind wing, dorsal view **21–24** holotype **21** supra-anal plate and paraprocts, dorsal view **22** left phallomere, dorsal view **23** subgenital plate and median phallomere, dorsal view **24** hook-like phallomere, dorsal view. Scale bars: 1.0 cm (**13, 14**), 0.5 mm (**15–20**), 1.0 mm (**21–24**).

and round; and 4) R3 (accessary median phallomere) large, while R3 (accessary median phallomere) somewhat reduced in *A. xizangensis*.

Measurements (mm). Male, pronotum: length × width 3.5–4.5, tegmina length: 14.1–14.8, overall length: 15.5–16.1.

Description. ***Male.*** Body yellowish brown with reddish (Figs 13, 14). Vertex brown. Face pale brown. Two spots on inter-antennae space reddish brown (Figs 14, 15). Antennae and maxillary palpi pale brown. Pronotal disc and hind margin reddish brown, lateral borders hyaline. Tegmina and wings pale yellow (Fig. 13). Legs translucent. Abdomen brown. Cerci yellowish brown (Fig. 14).

The distance between compound eyes narrower than that of antennae, ocelli border not obvious (Fig. 15). Curved macula under the antennal sockets. Third, fourth and the fifth maxillary palpi approximately same length (Fig. 17). Pronotum nearly triangular, width greater than length, the front and hind margins nearly straight, the posterolateral angle blunt and round, and disc with trapezoidal symmetrical white maculae (Fig. 16). Tegmina and hind wings fully developed, both extending beyond the end of abdomen (Fig. 13). Tegmina with M and CuA longitudinal, CuA with four branches (Fig. 19). Hind wings with M straight and simple; CuA with five complete branches (Fig. 20). Anteroventral margin of front femur type B_3 (Fig. 18). Pulvilli present only on the fourth tarsomere; tarsal claws symmetrical and unspecialized, arolia present.

Male abdomen and genitalia. Abdominal terga unspecialized. Supra-anal plate nearly triangular, hind margin slightly curled up. Paraproct plates simple (Fig. 21). Subgenital plate slightly asymmetrical, styli short and cylindrical, the right one slightly larger than the left, inter-styli margin concave (Fig. 23). Left phallomere complex, inverted Y-shaped (Fig. 22). Median phallomere stem club-shaped, basal part tapering, accessory median sclerite curved, base and apex all with short setae (Fig. 23). Hook on the right side, with pre-apical incision (Fig. 24).

Remarks. It can be distinguished from other species in this group by the light-colored pronotum.

Etymology. The meaning of the Latin word *alba* is white, referring to the white maculae on the pronotum.

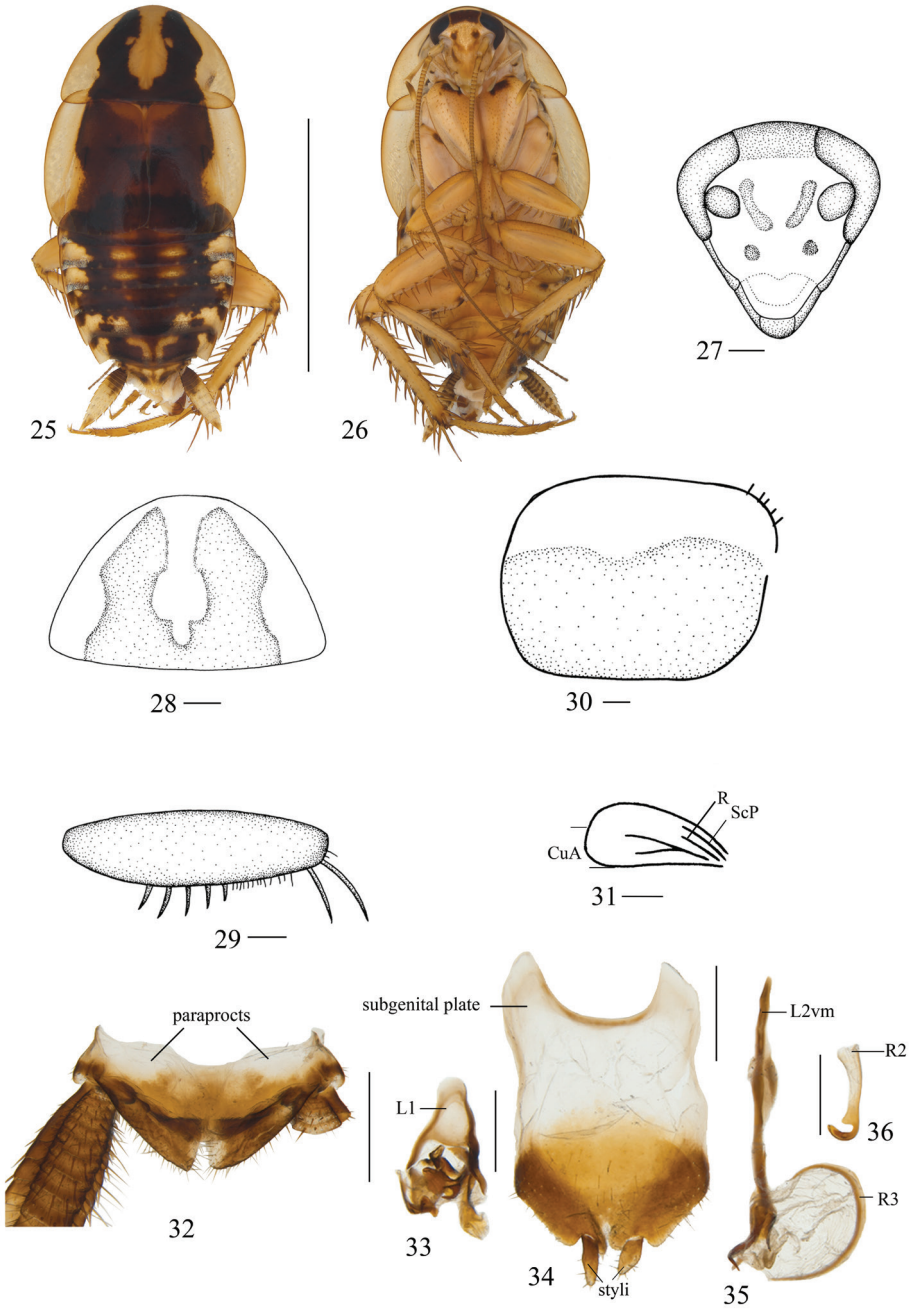
Distribution. China (Zhejiang).

Allacta hainanensis (Liu et al., 2017), comb. n.

Figs 25–36, 45

Temnopteryx hainanensis Liu et al., 2017: 179.

Type material examined. ***Holotype*** of *Temnopteryx hainanensis*, male (SHEM), CHINA, Hainan Province, Changjiang, Bawangling, 23–24-IX-2011, Xian-Wei Liu leg. ***Other material examined.*** CHINA, Hainan Province: 1 male and 2 females (SWU), Jianfengling, Mingfenggu, 23–28-IV-2015, Lu Qiu & Qi-Kun Bai leg. 1 male (SWU), Diaoluoshan, Lingshui, 1050m, 10-VIII-2010, Guo Zheng leg.



Figures 25–36. *Allacta hainanensis* (Liu et al., 2017), comb. n., male. **25** dorsal view **26** ventral view **27** head, ventral view **28** pronotum, dorsal view **29** front femur, ventral view **30** tegmen, dorsal view **31** hind wing, dorsal view **32** supra-anal plate and paraprocts, dorsal view **33** left phallomere, dorsal view **34** subgenital plate, dorsal view **35** median phallomere, dorsal view **36** hook-like phallomere, dorsal view. Scale bars: 1.0 cm (**25, 26**), 0.5 mm (**27–31**), 1.0 mm (**32–36**).

Diagnosis. This species can be easily distinguished from all other congeners by the much reduced tegmina and wings, which only reaching the third tergum. The coloration pattern (body light yellowish brown, with large brown areas dorsally) is also unusual in this genus (see Figs 25 and 45).

Measurements (mm). Male, pronotum: length × width 4.3–4.6 × 6.9–7.4, tegmina length: 5.5–5.7, overall length: 17.0–17.2; female, pronotum: length × width 4.3–4.5 × 5.7–6.5, tegmina length: 4.6–4.9, overall length: 12.6–13.1.

Description. ***Male.*** Body dark brown with yellowish (Fig. 25). Frons yellowish brown, vertex with dark brown bands. Antenna brown. The fifth of maxillary palpomere brown (Fig. 26). Pronotum yellowish brown, lateral and hind border translucent, and disc with two dark brown stripes and an irregular pale yellowish brown macula. Tegmina brown, the inner border dark brown, lateral border pale yellowish brown (Fig. 25). Legs pale yellowish brown. Abdominal terga brown, lateral margin with blackish brown spots. Cerci yellowish brown, base brown (Fig. 26).

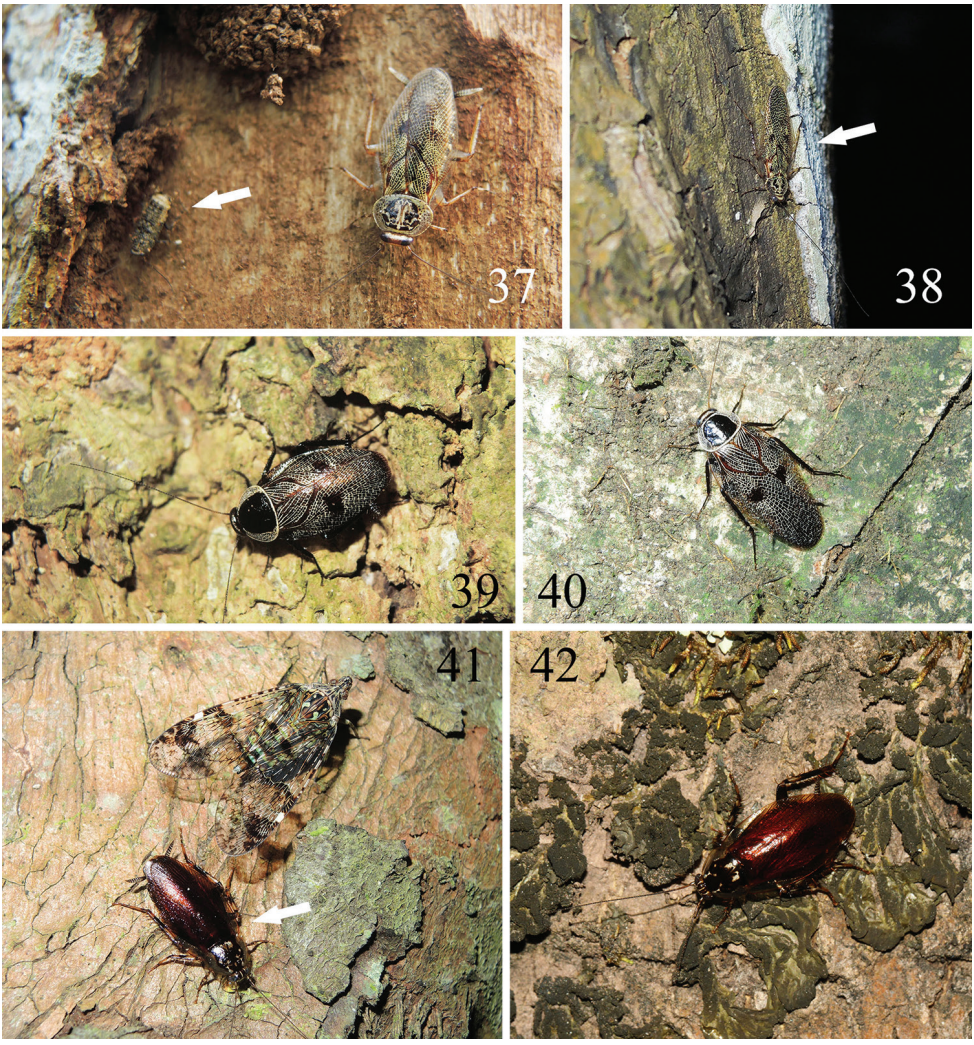
Vertex with interocular space obviously narrower than the distance between antennae sockets (Fig. 27). Third and fourth maxillary palpomeres approximately same length, and both significantly longer than the fifth. Pronotum nearly triangular, the front margin blunt and round; the hind margin nearly flat (Fig. 28). Tegmina and hind wings reduced; tegmina nearly quadrilateral, veins inconspicuous, only reaching the third tergum of the abdomen (Fig. 30); hind wings short and narrow, about half the length of the tegmina, and veins simple with two longitudinal veins (Fig. 31). Anteroventral margin of front femur type B_3 (Fig. 29). Hind legs first tarsus approximately same length to the sum of other four tarsomeres. Pulvilli present only on the fourth tarsomere, tarsal claws symmetrical and unspecialized, arolia present (Figs 25, 26).

Female similar to the male.

Male abdomen and genitalia. Abdominal terga unspecialized. Supra-anal plate nearly triangular, symmetrical, the middle of hind margin with incisions. Paraproct plates simple, similar, sheet-like, apex with scattered bristles (Fig. 32). Subgenital plate symmetrical, lateral margin curved and blunt; styli nearly cylindrical, arising in two concavities of hind margin; the right stylus slightly longer than the left; and the hind margin with W-shaped concave (Fig. 34). Left phallomere complex (Fig. 33). Median phallomere stem slender, bending near apex, apex sharp, base forked, median phallomere subsidiary sclerite C-shaped clavate, apex gradually sharper (Fig. 35). The hook-shaped phallomere on the right of subgenital plate, and the hook short (Fig. 36).

Remarks. Liu et al. (2017) placed this species in *Temnopteryx* and stated it resembles *T. dimidiatipes* Bolivar, 1890 from the Philippines. However, Princis (1957) erected *Lobopterella* and treated *T. dimidiatipes* as the type species. Thus *Lobopterella dimidiatipes* belongs to subfamily Blattellinae and does not display the characteristic of Pseudophyllodromiinae, viz. the hook-shaped phallomere on the right side (Roth 1988).

Through field efforts, we obtained several specimens with reduced tegmina and wings from Hainan Island. After comparing them with the type specimen (deposited in SHEM), we confirmed that our specimens are *Temnopteryx hainanensis* Liu et al., 2017. After dissecting the male genitalia, we found the hook-shaped phallomere of *Temnopteryx hainanensis* is on the right, and the pulvilli is present only on the fourth

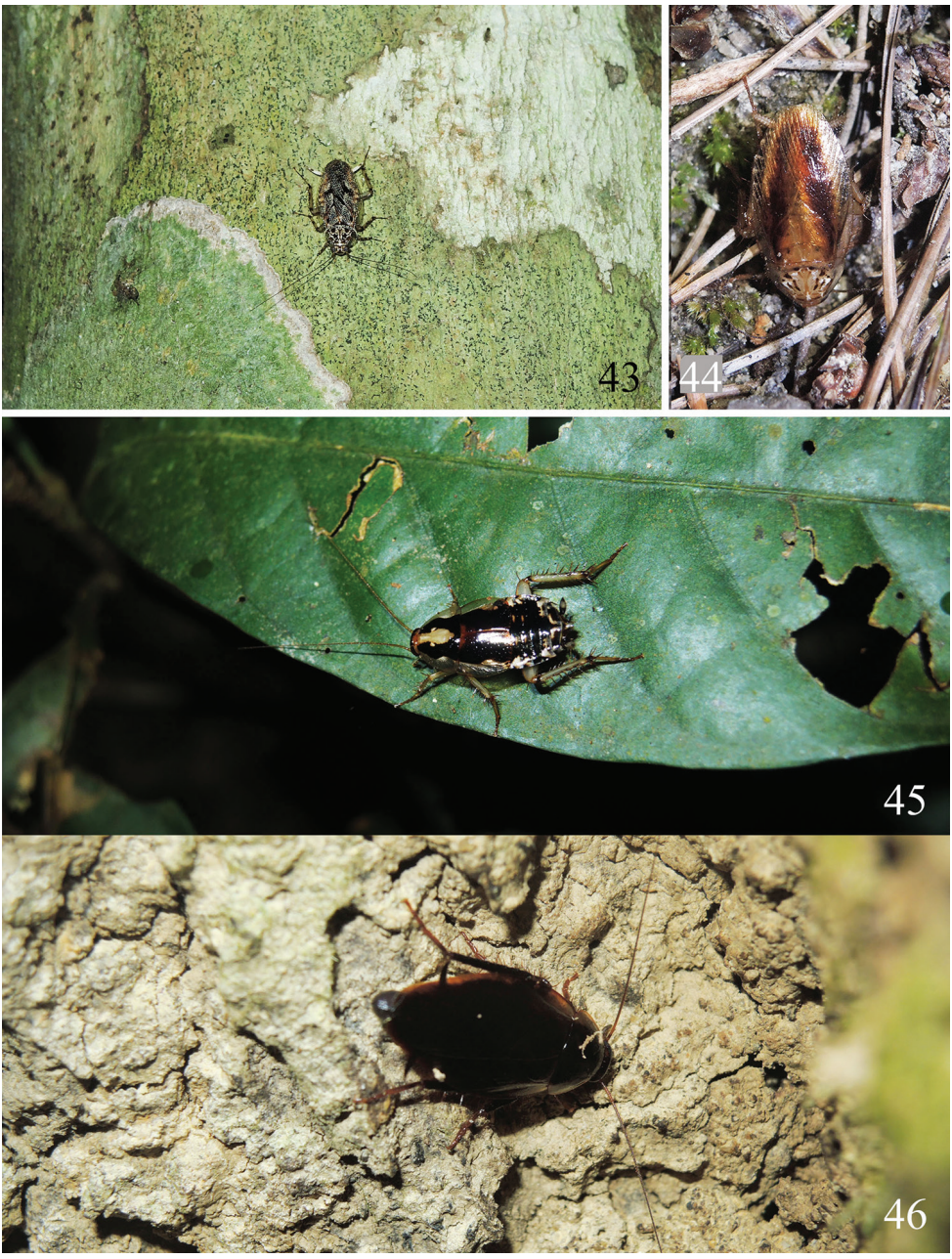


Figures 37–42. Habitats of *Allacta* species from China. **37, 38** *Allacta transversa* from Hainan **37** when we remove the tree bark, a crowd of *A. transversa* run away and only an adult and a nymph (white arrow) hold still (Baoting County) **38** a very flat adult (white arrow) disguises itself in its surroundings (Baoting County) **39, 40** *Allacta bimaculata* from South China **39** a female resting on tree trunk (Longzhou, Guangxi) **40** a male resting on tree trunk (Xishuangbanna, Yunnan) **41, 42** *Allacta robusta* from Pu'er, Yunnan **41** Individual (white arrow) found on the tree trunk along with a planthopper (Meizihu Lake, Simao) **42** Individual crawling on the tree trunk (Zhenyuan County). All photographs by Lu Qiu.

tarsomere, thus, *Temnopteryx hainanensis* should be placed in the pseudophyllodromiine genus *Allacta* as *Allacta hainanensis* (Liu et al., 2017) comb. n.

This species is placed in the *hamifera* species group by having two lobes which forming a keel-like ridge, and in having the dark portion of the pronotum reduced to two longitudinal bands.

Distribution. China (Hainan).



Figures 43–46. Habitats of *Allacta* species from China. **43** *Allacta ornata* found on tree trunk (Xishuangbanna, Yunnan) **44** most *Allacta xizangensis* were found on tree trunks during an expedition in VIII.2015, but this one is the only one found on the ground (Zayü County, Xizang) **45** a living *Allacta hainanensis* (Liu et al., 2017) comb. n. was found on the leaf (Jianfengling, Hainan) **46** a female *Allacta bruna* sp. n. (with ootheca) found on a tree trunk (Jianfengling, Hainan). All photographs by Lu Qiu.

Discussion

Previous studies indicated that *Allacta* species inhabit on tree trunks (Rentz 2014; Wang et al. 2014). Through our field investigations from 2014 to 2017, we found that most Chinese *Allacta* species are more likely to inhabit tree trunk surfaces or under the bark. Sometimes, individuals are also observed crawling on the leaves (Fig. 45) or ground (Fig. 44). *A. bimaculata*, *A. ornata*, *A. robusta*, *A. transversa*, *A. bruna* sp. n., and *A. xizangensis* are observed resting on tree trunks. Their bodies are maculated (except for *A. bruna* sp. n.), and some species even have reticulated mottling on the tegmina (e.g., *A. bimaculata*, *A. ornata*, *A. transversa*), which provide an excellent disguise on a tree trunk surface that is covered with lichens and mosses (Figs 37–43). In the daytime, *Allacta* individuals may hide under the bark (Fig. 37), while during the night, they will come out and crawl on the trunk. When approaching them, they would not act dead or fall down to the ground, but instead hide from the collectors. They can move transversely somewhat like crab and very rapidly slip away to the opposite side of the trunk to escape from being captured. While when the collectors continue tracking them, they will move around to the other side of the trunk, or go to a higher level on the trunk. Characters such as the presence of pulvilli only on the fourth tarsomere and spines on the other 3 tarsomeres help *Allacta* species efficiently move about on the trunk. They can conduct such fast transverse actions probably because they only walk or climb "on tiptoe" (Wang et al. 2014).

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Revision of world *Sphecomyia* Latreille (Diptera, Syrphidae)

Kevin M. Moran[1,2], Jeffrey H. Skevington[1,2]

1 *Canadian National Collection of Insects, Arachnids and Nematodes, Agriculture and Agri-Food Canada, 960 Carling Avenue, Ottawa, ON K1A 0C6, Canada* **2** *Carleton University, Department of Biology, 1125 Colonel By Drive, Ottawa, Ontario K1S 5B6, Canada*

Corresponding author: *Kevin M. Moran* (syrphidae@kevinmoran.com)

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Abstract

The 16 world species of *Sphecomyia* Latreille are revised, including seven previously undescribed species (*S. cryptica* Moran, **sp. n.**, *S. hoguei* Moran, **sp. n.**, *S. interrupta* Moran, **sp. n.**, *S. oraria* Moran, **sp. n.**, *S. pseudosphecomima* Moran, **sp. n.**, *S. sexfasciata* Moran, **sp. n.**, and *S. weismani* Moran, **sp. n.**). Descriptions, redescriptions, male genitalia photographs, distribution maps, and an illustrated key for all *Sphecomyia* are presented. DNA barcode data are provided for all 16 species with a cytochrome oxidase subunit I gene tree presented and discussed. *Sphecomyia* **stat. rev.** is redefined to represent the monophyletic lineage of species within subtribe Criorhinina possessing a bare, medial vitta extending ventrally from the oral margin in both sexes, a bare gena, a bare katepimeron, a scutellum with at least anterior margin densely pruinose, an anterior ventral half of vein C before crossvein h without setae, and a narrow intersection of vein R_1 with vein C. Three species groups of *Sphecomyia* are identified: the *S. vittata* group which possess pruinose scutellar vittae, the *S. pattonii* group which lack pruinose scutellar vittae, and *S. metallica* (Bigot), a hairy bee mimic with a completely pruinose scutum. *Criorhina tsherepanovi* Violovitsh is resurrected and transferred, along with *Criorhina aino* Stackelberg, to the genus *Sphecomyia*: *S. tsherepanovi* (Violovitsh), **comb. n.** and *S. aino* (Stackelberg), **comb. n.** *Criorhina metallica* (Bigot) is designated as the senior synonym of *C. lupina* (Williston), not junior as improperly treated, and transferred to *Sphecomyia*: *S. metallica* (Bigot), **comb. n.** The species *Sphecomyia fusca* Weisman, *S. nasica* Osburn, and *S. occidentalis* Osburn are transferred to *Criorhina* Meigen: *C. fusca* (Weisman), **comb. n.**, *C. nasica* (Osburn), **comb. n.**, and *C. occidentalis* (Osburn), **comb. n.**

Keywords

Criorhina, description, DNA barcode, flower fly, hoverfly, identification key, new species, species group, taxonomy

Introduction

Sphecomyia Latreille, 1829 (Diptera, Syrphidae), wasp fly in ancient Greek, is a Holarctic genus of large, predominantly wasp mimics placed within Eristalinae: Milesiini: Criorhinina (Thompson 1972a, 1972b). Members possess the classic, anteroventrally produced face predominant throughout the subtribe Criorhinina. Little is known of their natural history outside of scattered floral and mating records. Larval habitat is unknown with larvae never illustrated or described, though it is likely similar to other Criorhinina in that they live in rot holes, decaying wood or roots. Within the Criorhinina, generic concepts are in dire need of review. Two genera, *Criorhina* Meigen, 1822 and *Sphecomyia*, are particularly in need of attention. Traditionally, bee mimic species were placed in the genus *Criorhina* and wasp mimic species in the genus *Sphecomyia*. This hypothesis has never been tested.

Penney et al. (2012) found a strong positive relationship between mimetic fidelity and body size. This supports the relaxed-selection hypothesis, suggesting that reduced predation pressure on less profitable prey species limits the selection for mimetic perfection. *Sphecomyia*, and Criorhinina in general, are large syrphids and profitable prey targets. Thus, according to this hypothesis, they likely experience intense pressure to evolve perfect mimicry which raises the possibility that these gestalts could be convergent and these genera paraphyletic. Therefore, a dedicated review of *Sphecomyia* is a necessary step in the testing of this hypothesis.

For most of *Sphecomyia*'s history, authors considered the genus more or less related to *Temnostoma* Lepeletier and Serville, 1828, another wasp mimic genus (Williston 1886; Shannon 1922; Hull 1949). Stackelberg (1930) was the first to hypothesize that a close relationship existed between *Criorhina* and *Sphecomyia* based upon the shared characteristic of an anteroventrally produced face. Thompson (1972a, 1972b) was the second to recognize a relationship between *Criorhina* and *Sphecomyia* based primarily on shared characteristics of an anteroventrally produced face, segmented aedeagus and pilose metasternum. Shatalkin (1975) provided further support for this relationship stating the genera were "remarkably similar in the structure of the hypandrium and surstyli and especially in the capsule of the aedeagus, which has well expressed lateral wings and inner lobes that are not fused."

Much of our knowledge about *Sphecomyia* was provided by Weisman who reviewed the genus over a series of four papers (Weisman 1964, 1965, 1966a, 1966b). Before Weisman, several authors (Williston 1886; Osburn 1908; Shannon 1925; Curran 1932) described species and provided dichotomous keys for existing species.

The first of the Weisman papers (Weisman 1964) involved the description of the species *Sphecomyia fusca* Weismann, 1964. The second work (Weisman 1965) examined male genitalia of known *Sphecomyia* and provided a dichotomous key to species based upon them. In this paper, Weisman split *Sphecomyia* into two major groupings of species: the *S. occidentalis* group (including *S. fusca*, *S. nasica* Osburn, 1908, and *S. occidentalis* Osburn, 1908), characterized by the absence of a dorsal horn on the basiphallus and a keeled, laterally sclerotized phallapodeme; and the *S. vittata* group (with *S. brevicornis* Osten Sacken, 1877, *S. columbiana* Vockeroth, 1965, *S. dyari* Shannon,

1925, *S. pattonii* Williston, 1882, *S. vespiformis* (Gorski, 1852), and *S. vittata* (Wiedemann, 1830)), characterized by a dorsal horn on the basiphallus and a unkeeled, rod-shaped phallapodeme. Weisman's third paper (Weisman 1966a) outlined species distributions and his final paper (Weisman 1966b) provided a synoptic description of the genus and species, and their taxonomic history.

In the present study we review and expand upon Weisman's foundation. We describe seven new species of *Sphecomyia*, provide habitus and genitalia photographs for all of the species, and provide the first key to the group since Weisman (1966b).

Figure 1. *Sphecomyia vittata* (Wiedemann, 1830).

Materials and methods

A list of material examined is provided. For the redescribed species, the examined material is available in a supplementary file. All specimens are labelled with a unique reference number, either with their unique collection number or in the format KMMXXXX. Label data from the studied individuals were transcribed by hand into the online CNC database and can be accessed at https://cnc.agr.gc.ca/. Specimens were borrowed from the following institutions:

AMNH	American Museum of Natural History, New York, New York, USA
ANSP	Academy of Natural Sciences, Philadelphia, Pennsylvania, USA
CAS	California Academy of Sciences, San Francisco, California, USA
CNC	Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, Ontario, Canada
CSCA	California State Collection of Arthropods, Sacramento, California, USA
CSUC	Colorado State University, Fort Collins, Colorado, USA

EMEC	Essig Museum of Entomology, University of California, Berkeley, California, USA
INHS	Illinois Natural History Survey, Champaign, Illinois, USA
JVSPC	Jeroen Van Steenis Personal Collection
LACM	Los Angeles County Museum of Natural History, Los Angeles, California, USA
MEMU	Mississippi State University, Mississippi, USA
MZH	Finnish Museum of Natural History, Helsinki, Finland
NBMB	New Brunswick Museum, St. John's, New Brunswick, Canada
NSPM	Nova Scotia Museum, Halifax, Nova Scotia, Canada
RBCM	Royal British Columbia Museum, Victoria, British Columbia, Canada
RMNH	Naturalis Biodiversity Centre, Leiden, Netherlands
SEMC	Snow Entomological Museum, University of Kansas, Lawrence, Kansas, USA
UBCZ	Spencer Museum, University of British Columbia, Vancouver, British Columbia, Canada
UCDC	R.M. Bohart Museum of Entomology, University of California, Davis, California, USA
UCRC	Entomology Research Museum, Department of Entomology, University of California, Riverside, California, USA
USNM	National Museum of Natural History, Washington D.C., USA
WIRC	University of Wisconsin Insect Research Center, Department of Entomology, University of Wisconsin, Madison, Wisconsin, USA
WSU	Maurice T. James Entomological Collection, Washington State University, Pullman, Washington, USA

Terminology, photography, measurement, and figures

Morphological terminology follows Cumming and Wood (2017). Plant systematics follows The Plant List (2013). Morphological features of Nearctic species were examined using an Olympus SZ60 and a Zeiss SteREO DiscoveryV12 stereo microscope. Whole habitus photographs of pinned specimens were taken using the base and StackShot parts of Visionary Digital Passport II system, an Olympus OM-D EM-5 Micro 4/3 camera, and a 60 mm f2.8 macro lens (equivalent to 120 mm focal length in 35 mm photography). The specimens were illuminated by a Falcon FLDM-i200 LED dome-light. Palaearctic specimens were examined and photographed using a Leica M205-C stereoscope equipped with a Leica DFC 450 module and using 0.6× (habitus) and 1.6× (genitalia) lenses. Final images were assembled using Zerene stacker (Littlefield 2018). Photographs and descriptions are not restricted to primary types and represent our species concepts as a whole.

Male genitalia were detached after relaxation of specimen in a moisture chamber and then macerated in heated lactic acid overnight before examination and photography.

Specimen measurements were taken using the Leica measurement module in Leica Application Suite and are based upon the smallest and largest specimen of each species. Body measurements represent the distance between the frons and the posterior end of tergite 4. Wing measurements represent the distance between the tegula and the apex of the wing. Measurements of antennal segments are approximations based on the mid-line of inner surface and are presented in the ratio format scape:pedicel:flagellomere. Maps include points from all specimens examined and were produced using Simplemappr (Shorthouse 2010).

In the description of type labels the contents of each label are enclosed within double quotation marks (“ ”), while italics denote handwriting, and the individual lines of data are separated by a double forward slash (//). At the end of each record, between square brackets ([]) and separated by a comma, the number of specimens and sex, the unique identifier or number and the holding institution are given.

DNA sequencing

The right midleg was removed from selected specimens. Some legs were sent to the University of Guelph Biodiversity Institute of Ontario for sequencing of the 5¢ end of the cytochrome *c* oxidase subunit I mitochondrial gene (COI), or Barcoding region, following protocols published in (Hajibabaei et al. 2005). Others were processed in house at the Canadian National Collection of Insects (CNC) by Scott Kelso using a modified version of the same protocol with custom primers (see Table 1).

These custom primers, COI-FX-A-R, B-F, B-R, and C-F are designed to sequence the Barcoding region in three portions, labeled A, B, and C after the primers, increasing the chance of successfully sequencing heavily fragmented DNA. This enabled sampling of species for which the only available material was older than 20 years, generally considered unsuitable for barcoding.

For material sequenced at CNC, raw sequence reads were scored using Sequencer 5.4.6 (2018) and aligned together with downloaded BOLD data using MAFFT (Katoh and Standley 2013).

All sequence data obtained are stored online on the BOLD database (www.boldsystems.org). They are publicly accessible on Genbank or in the *Sphecomyia* of the World (SPHEC18) dataset available at http://www.boldsystems.org/index.php/Public_SearchTerms?query=DS-SPHEC18.

Table 1. Cytochrome c Oxidase I mitochondrial gene primers.

Primer name	Primer design	Primer sequence
Heb-F	Folmer et al. 1994	GGT CAA CAA ATC ATA AAG ATA TTG G
COI-Fx-A-R	Kelso (in prep)	CGD GGR AAD GCY ATR TCD GG
COI-Fx-B-F	Kelso (in prep)	GGD KCH CCN GAY ATR GC
COI-Fx-B-R	Kelso (in prep)	GWA ATR AAR TTW ACD GCH CC
COI-Fx-C-F	Kelso (in prep)	GGD ATW TCH TCH ATY YTA GG
COI-780R	Gibson et al. 2011	CCA AAA AAT CAR AAT ARR TGY TG

Data analysis

Neighbor-joining, utilizing PAUP 4.0a163 (Swofford 2001) with default values, was used to explore morphological species concepts for ingroup taxa. *Blera fallax* (Linnaeus, 1758), *Milesia virginiensis* (Drury, 1773), *Temnostoma alternans* Loew, 1864, and *Xylota flavifrons* Walker, 1849, which also belong to Milesiini, were used as outgroups outside of Criorhinina. For outgroups inside Criorhinina, we included any described species for which we possessed a barcode.

Taxa in the tree are labeled in the following format BOLD Process ID | Taxon Name | Institution Sample ID.

Results

Key to *Sphecomyia* species

1 Hairy-bee mimic; scutum completely pruinose (Figs 16E, 17E) ..... ***metallica* (Bigot)**

– Wasp mimic; scutum mostly non-pruinose with distinct regions of pruinosity (Figs 7, 10, 16A–D, 16F) **2**

2 Thoracic scutum without pruinose vittae (Figs 7, 10); fore tarsi broadened (Fig. 6A) **7**

– Thoracic scutum with pruinose vittae (Figs 16A–D, F); fore tarsi not broadened (Fig. 6B) **3**

3 Antenna not elongated, shorter than depth of head in lateral view (Fig. 5A, B) **5**

– Antenna elongated, longer than depth of head in lateral view (Fig. 5C) **4**

4 Anepimeron pruinose (Fig. 19A); sternite 2 with anterior corners and lateral margins pruinose (Fig. 21D) ..... ***vittata* (Wiedemann)**

– Anepimeron not pruinose (Fig. 19B); sternite 2 completely black or with faint, interrupted, pruinose band anteriorly (Fig. 21E) ***vespiformis* (Gorski)**

5 Thoracic scutum with six pruinose vittae (supra-alar area pruinose in dorsal view) (Fig. 16B) ..... ***sexfasciata* sp. n.**

– Thoracic scutum with four pruinose vittae (supra-alar area without pruinosity) (Fig. 16A, C) **6**

6 Scutellum completely pruinose, no black rim posteriorly (Fig. 22B); medial facial vitta interrupted by a spot of pruinosity on the tubercle (Fig. 4A); antennal segments roughly in a 3:3:2 ratio (Fig. 5A) ..... ***interrupta* sp. n.**

– Scutellum not completely pruinose, with black rim posteriorly (Fig. 22A); medial facial vitta entirely non-pruinose (as in Fig. 4C); antennal segments roughly in a 2:2:1 ratio (Fig. 5B) ..... ***brevicornis* Osten Sacken**

7 Tergite 2 with a single grey, medially-interrupted band, placed medially in the tergite (Fig. 10B–D) **14**

– Tergite 2 with two yellow bands: the anterior interrupted, placed medially in the tergite, and the posterior, along posterior tergal margin, uninterrupted (Fig. 7) **8**

8 Tergite 1 pruinose only in posterolateral corners (Figs 10A, 11A) ..... ***columbiana* Vockeroth**

– Tergite 1 with uninterrupted, pruinose band along posterior margin (Figs 7, 11B) **9**

9 Ventral calypter with long, black pile (Fig. 20B) ..... ***pattonii* Williston**

– Ventral calypter with long, yellow pile (Fig. 20A) **10**

10 Anterior two-thirds of scutellum pruinose (Fig. 22D) ..... ***weismani* sp. n.**

– Only anterior third or less of scutellum pruinose (Fig. 22E) **11**

11 Scutellum completely black pilose (Fig. 15B); sternites 2–4 mostly pruinose, with shiny to dull black narrow anterior border and transverse subapical band that reaches lateral sides of sternite (Fig. 21C) ..... ***oraria* sp. n.**

– Scutellum at least partly yellow pilose (Fig. 15A); sternites 2–4 almost completely pruinose, with at most a triangular region of non-pruinosity posteromedially (Fig. 21A, B) **12**

12 Sternites 2–4 with a posteromedial, triangular non-pruinose (shiny) region of the same size approximately (Fig. 21A); surstyli about twice as long as broad (Fig. 9C) ..... ***cryptica* sp. n.**

– Sternites 2–4 with a posteromedial, triangular non-pruinose region of different size, smaller on ensuing sternites (Fig. 21B); surstyli more than three times longer than broad (Fig. 9A, B) **13**

13 Narrowest part of surstylus about one fourth the width of base (Fig. 9A) ..... ***dyari* Shannon**

– Narrowest part of surstylus about half the width of base (Fig. 9B) ..... ***hoguei* sp. n.**

14 Cell c bare only on basal third ..... ***pseudosphecomima* sp. n.**

– Cell c bare on basal two-thirds **15**

15 Ocellar triangle mostly pale pilose; silver-yellow pruinosity on face, thorax and abdomen; antennal segments pale pilose (Fig. 13A); aedeagus as in Fig. 2A ..... ***aino* (Stackelberg)**

– Ocellar triangle mostly dark pilose; silver-white pruinosity on face, thorax and abdomen; antennal segments black pilose (Fig. 13B); aedeagus as in Fig. 2L ..... ***tsherepanovi* (Violovitsh)**

***Sphecomyia* stat. rev.**
Figs 1, 2A–F, 2J, 3B, 4–27

Sphecomye Latreille 1825: 495.
Sphecomyia Latreille in Bory 1829: 545 (also Latreille 1829: 495) – Williston 1886: 256; Osburn 1908: 14; Shannon 1925: 43; Curran 1932: 8; Stone 1965: 612; Weisman 1965: 265, 1966a: 50, 1966b: 189; Vockeroth and Thompson 1987: 736. Type species: *Chrysotoxum vittatum* Wiedemann 1830 by subsequent designation of Macquart 1842.
Epopter Wiedemann 1830: 91. Synonymy in Evenhuis and Pont 2013: 28. Type species: *Psarus ornatus* Wiedemann, 1830 [= *Sphecomyia vittata* (Wiedemann, 1830)], by monotypy.
Tyzenhausia Gorski 1852: 172. Synonymy in Wahlberg, 1854: 155. Type species: *Tyzenhausia vespiformis* Gorski 1852, by original designation.
Eurhinomallota Bigot 1882: 78. Type species: *Eurhinomallota metallica* Bigot 1882 by original designation. Syn. n.
Eurhynomallota Bigot 1883: 225. Unjustified emendation of *Eurhinomallota*.
Eurinomallota Kertész 1910: 62. Unjustified emendation of *Eurhinomallota*.
Brachymyia Williston 1882a: 77 – Williston 1882b: 330; Shatalkin 1975: 131. Type species: *Brachymyia lupina* Williston 1882, by original designation. Syn. n.

Diagnosis. Male dichoptic. Both sexes with bare, medial vitta extending ventrally from oral margin, usually to base of antenna, except interrupted by pruinosity at facial tubercle in *S. interrupta* and only extending to facial tubercle in *S. metallica*. Gena bare. Katepimeron bare. Scutellum with at least anterior margin densely pruinose. Narrow intersection of vein R_1 with vein C. Anterior ventral half of vein C before crossvein h without setae. Distance between apices of veins R_1 and R_{2+3} longer than distance between apices of veins R_{2+3} and vein R_{4+5}+M_1. Abdominal pile erect. Phallapodeme banana-shaped.

Redescription. Male. Body length: 9.2–17.1 mm. Wing length: 7.7–12.1 mm. ***Head.*** Face black, bare, concave beneath antenna, produced downwards and pruinose except with bare, medial vitta extending from oral margin, usually to base of antenna, except interrupted by pruinosity at facial tubercle in male *S. interrupta* Moran sp. n., and only extending to facial tubercle in male *S. metallica* (Bigot, 1882) or just beyond in the female; gena broad, as broad or broader than long, bare, shiny; anterior tentorial pit short, extending along ventral one-third of eye, pilose; frontal prominence distinct; frons broad, of variable size, at least partially pruinose; vertex variable in shape and pruinosity; ocellar triangle pilose, small; eye bare; male dichoptic; antenna length variable; kidney-shaped basoflagellomere, except sub-triangular in *S. brevicornis*, *S. vespiformis* and *S. vittata*, with bare arista dorsally placed.

Thorax. About as long as broad, short pilose except in *Sphecomyia metallica*; postpronotum pilose; proepimeron pilose; anterior anepisternum bare, posterior anepisternum pilose; scutum with or without pruinose vittae; scutellum with at least anterior

margin densely pruinose, without apical sulcus and with ventral pile fringe; katepisternum bare anteriorly, discontinuously pilose posteriorly with broadly separated patches; anepimeron with anterior portion pilose, and dorsomedial and posterior bare; katepimeron bare; metathoracic pleuron bare; without hypopleural pile at the base of the posterior thoracic spiracle; meron bare, except variable pilose in *S. vespiformis*; metathoracic spiracle about same size as flagellum; metasternum pilose; postmetacoxal bridge incomplete; plumula simple, elongate, short, not reaching calypteral margin; calypter yellow.

Legs. Coxae pilose anteriorly, bare posteriorly; hind coxa pruinose anteriorly; metafemur narrow, at most slightly swollen, without basoventral setose patch; metatibia transverse apically, rounded basoventrally.

Wing. Hyaline; stigmatic crossvein present; crossvein r-m at outer fourth of cell dm; anterior ventral half of vein C before crossvein h without setae (Fig. 3B); narrow intersection of vein R_1 with vein C (Fig. 3B); distance between apices of veins R_1 and R_{2+3} longer than distance between apices of veins R_{2+3} and R_{4+5}+M_1 (Fig. 3B); cell r_{2+3} open; vein R_{4+5} straight; vein R_{4+5}+M_1 no longer than crossvein h; vein M_2 absent; vein CuP+CuA short, curved.

Abdomen. Oval, slightly longer than broad, often with pruinose bands; abdominal pile erect.

Male genitalia. Surstyli symmetric; aedeagus segmented, with phallapodeme separated from basiphallus and distiphallus; phallapodeme banana-shaped (Fig. 2A–O); well-developed ctenidion.

Female. As in male, except for usual sexual dimorphism.

Distribution. 13 Nearctic (12 Western, 1 Eastern) and 3 Palaearctic species.

Remarks. Latreille (1825) first referenced the genus in French vernacular as *Sphecomye* based on specimens collected in Carolina by D. Bose. No description was included, nor was a specific epithet assigned to the specimens, thus the name is considered unavailable. Stark (1828) provided a translation from French vernacular as *Sphecomyia*, but as it referenced Latreille (1825) it still is not considered available. *Sphecomyia* is first made available in Latreille (1829) in which description of the genus is provided. Macquart (1842) designated *Chrysotoxum vittatum* Wiedemann as the type species by monotypy.

In this paper, *Sphecomyia* is redefined as the monophyletic unit of species within Criorhinina that possess the following characters: a bare, medial vitta extending ventrally from the oral margin in both sexes, a bare gena, a bare katepimeron, a scutellum with at least anterior margin densely pruinose, an anterior ventral half of vein C before crossvein h without setae and a narrow intersection of vein R_1 with vein C. While the combination of characters used to define *Sphecomyia* is unique, the subtribe Criorhinina is rife with homoplasy and the presence of one or more of these character states without all the others should not be taken as an indication a species belongs in *Sphecomyia*.

Brachymyia Williston, 1882 and *Eurhinomallota* Bigot, 1882 are newly synonymized with *Sphecomyia* as the type species of both genera fall within this definition and are combined with it as a result of this change. This decision is further supported

by molecular evidence showing a close relationship with *Sphecomyia*, i.e., the present COI gene tree and a multi-gene molecular phylogeny of the Criorhinina which will be presented in an upcoming paper. It is the authors opinion that combination with *Sphecomyia*, as opposed to resurrecting the concept as a monotypic genus, serves to emphasize its relationship with the group.

There are three major, monophyletic lineages of *Sphecomyia*. The *vittata* group, composed of the species with pruinose vittae on the scutum, i.e., S. *brevicornis*, *S. interrupta* sp. n., *S. sexfasciata* Moran sp. n., *S. vespiforme*, and *S. vittata*. Secondly, the *pattonii* group comprised of species with broadened fore tarsi and without pruinose vittae on the scutum, i.e., *S. aino* (Stackelberg, 1955), *S. cryptica* Moran sp. n., S. dyari, *S. hoguei* Moran sp. n., *S. oraria* Moran sp. n., *S. pattonii*, *S. pseudosphecomima* Moran sp. n., *S. tsherepanovi* (Violovitsh, 1973), and *S. weismani* Moran sp. n. The third group comprises only one species, *Sphecomyia metallica*, which has a completely pruinose scutum. *S. metallica* shares several characters with the *vittata* group. It has elongated surstyli, with a rounded baso-ventral lobe, reminiscent of the *vittata* group and it lacks the broadened fore tarsi of the *pattonii* group. Morphological characters of *Sphecomyia* are discussed in greater detail in the morphology section (see below).

Also of note, Shatalkin (1975) redefined *Brachymyia* as representing the species of *Criorhina* which lack a ventral scutellar fringe and possess hypopleural pile. The type of *Brachymyia*, *Sphecomyia metallica*, does not fit this generic definition as it has a ventral scutellar fringe and lacks hypopleural pile. Neither *Criorhina berberina* (Fabricius, 1805) nor the other species Shatalkin combined with *Brachymyia* are closely related to the type. Definitions of other criorhinine genera might change after this work.

Sphecomyia aino (Stackelberg, 1955), comb. n.

Figs 2A, 10B, 12B, 13A, 14B, 24

Penthesilea aino Stackelberg 1955: 347. Type locality: Russia: Far East, Sakhalin Central Experimental Station. [ZISP]

Criorrhina stackelbergi Violovitsh 1973: 112. Type locality: Russia: Siberia, Altai Mts. [ZISP]

Criorhina stackelbergi Violovitsh 1976:341 – 1982: 211, 1983: 137; Peck 1988:207.

Criorrhina aino Mutin and Barkalov 1990: 118.

Criorhina aino Mutin and Barkalov 1997: 217 – Gritskevich 1998: 11; Barsukova 2012: 187 Mutin et al. 2016: 9; Mutin and Barkalov 2016: 21.

Diagnosis. Species similar to *S. pseudosphecomima* or *S. tsherepanovi* but can be distinguished by the following characters: cell c bare on basal two-thirds; ocellar triangle pale pilose; silver-yellow pruinose; basiphallus as in Fig. 2A.

Redescription. Male. Body length: 10.0 to 13.5 mm. Wing length: 8.2 to 8.4 mm. ***Head.*** Face silver-yellow pruinose with shiny, black, medial vitta extending from oral margin to base of antenna; frons broad, about as long as broad at antenna, two-thirds as broad at vertex as at antenna, bare, with silver-yellow pruinosity along posterior rim;

vertex triangular, longer than broad, shiny, with ocellar triangle pale pilose; postocular border silver-yellow pruinose; postocular pile black; occipital pile pale; male narrowly dichoptic; antenna black, pale pilose, with length of segments roughly in a 3:3:2 ratio.

Thorax. Sub-shiny black; postpronotum pale pilose, scutum pale pilose, except with black pile posteromedially; scutellum, postalar callus, proepimeron pale pilose, posterior anepisternum pale pilose; posterior katepisternum pale pilose with broadly separated patches; anterior anepimeron, metasternum pale pilose; postpronotum, anterior eighth of scutellum, broad posterior margin of anepisternum and dorso-posterior corner of katepisternum silver-yellow pruinose; area between postpronota weakly silver-yellow pruinose, except shiny medially; anepimeron shiny; scutum without pruinose vittae; ventral calypter with long pale pile.

Legs. Foreleg black, except reddish-yellow at apex of femur; fore tarsi slightly broadened; midleg yellow, except basal four-fifths of femur and last two tarsomeres black; hind leg reddish-yellow, except last two tarsomeres black; legs pale pilose, except black pilose on fore tibia, fore tarsi, extreme apex of fore femur and last two mid and hind tarsomeres; hind coxa silver-yellow pruinose.

Wing. Hyaline; microtrichia absent from following areas: cell bc; basal two-thirds of cell c; basal fourth of cell sc; cell r_1 from base almost to crossvein r-m; broad basal portion of cell br (before origin of M) and about basal two-fifths of narrower portion of this cell (caudad of spurious vein only); cell bm, except apex and narrow anterior and posterior margins of about apical fourth; broad anterior margin of cell cua; narrow, elongate, oval area proximal to vein A_1.

Abdomen. Tergites and sternites shiny to sub-shiny, black with silver-yellow pruinosity as follows: tergite 1 pruinose posteriorly; tergite 2 with thin, interrupted, medial band which curves posteriorly to reach the posterolateral corners; tergite 3 with thin, medial, interrupted band which does not curve anteriorly; tergite 4 with similar but thinner band; sternite 1 weakly pruinose; sternites 2 and 3 pruinose on anterior third and sub-shiny black on remainder; sternite 4 with anteromedial pruinose spots; pile of abdomen pale.

Male genitalia. Surstylus not elongated, about as long as broad, curving upward ventrally; pilose on anterolateral outer surface of surstylus; minute spines on ventral surface and apical half of interior lateral surface; basal fourth of ventral surface of the surstylus produced into a lobe directed anteriorly, with minute pubescence on ventral and lateral inner surface; cerci rounded, with no invagination on posterior border; aedeagus as in Fig. 2A.

Female. Similar to male except normal sexual dimorphism.

Distribution. Far Eastern Russia including Sakhalin Island and westerly into Eastern Siberia (Fig. 24).

Biology. Collected visiting flowers of *Cornus alba* (L.) Opiz, *Weigela middendorffiana* C. Koch, *Rhododendron aureum* Georgi, and *Rhododendron dauricum* L. Known to hilltop. Recorded flying in June and July.

Remarks. Two morphospecies are recognized in the *Sphecomyia aino* complex, *S. aino* from continental East Palaearctic and S. ts*herepanovi* from the Japanese and Kuril Islands. *Sphecomyia aino* are silver-yellow pruinose with mostly pale pile on their an-

tennal segments and ocellar triangle. *Sphecomyia tsherepanovi* are silver-white pruinose with mostly black pile on their antennal segments and ocellar triangle. Additionally, the two populations were found to possess differently shaped dorsal horn on their basiphallus (Fig. 2A, L). We argue that these character differences, along with the 3% difference in the DNA barcode between the two taxa, especially considering that the mainland population has little to no variation in COI even across distances greater than 3000 km, are significant enough to warrant separation into two distinct species.

Of note are a male and female pair of specimens collected together in mainland Russia. Both possess characters associated with *S. tsherepanovi*. They are silver-white pruinose. The female is fully black pilose on its antennal segments and ocellar triangle, while the male is mixed pale and black pilose on these regions. The basiphallus of the male is identical to that of Fig. 2A. Both were barcoded, with Folmer regions identical to *S. aino* recovered. We consider this pair aberrant and not representative of *S. aino*. The male appears teneral as its exoskeleton is light brown in color. The female has a completely black pilose scutum and face along with a mixed pale and black pilose scutellum. These characters are not seen in another specimen of either species and may be indicative of a mutation. It is also is possible the female is teneral. Lending support to this hypothesis is communication with Russian Syrphidae researcher Valery Mutin who indicates all local specimens he collected fit the typical *S. aino* morphospecies concept. Still it is possible, though unlikely, that these specimens indicate that the mainland species is more variable than we have come to believe.

Sphecomyia brevicornis **Osten Sacken, 1877**

Figs 2B, 5B, 16A, 17A, 18A, 21G, H, 22A, 23

Sphecomyia brevicornis Osten Sacken 1877: 341 – Röder 1879: 97; Williston 1882b: 328, 1886: 258; Aldrich 1905: 404; Osburn 1907: 4, 1908: 11; Kertész 1910: 348; Cole and Lovett 1921: 293; Shannon 1925: 43; Hull 1949: 264; Stone et al. 1965: 612; Weisman 1965: 266, 1966a: 51, 1966b :193; Boyes and van Brink 1967: 432, 1970: 212; Cole and Schlinger 1969: 331; Telford 1975: 21. Type locality: Webber Lake, Sierra County, California. [MCZ]

Sphecomyia vespiformis of Curran 1932: 8, not Gorski 1852. Misidentification.

Diagnosis. Species most similar to *S. interrupta* sp. n. and *S. sexfasciata* sp. n. but can be distinguished by the following characters: scutum with two pairs of pruinose vittae; cell c completely microtrichose; antenna possessing a 2:2:1 ratio of segments; frons bare; anepimeron not pruinose; anterior three-fourths of scutellum pruinose; medial facial vitta not interrupted by a spot of pruinosity.

Redescription. Male. Body length: 11.0–16.0 mm. Wing length: 9.7–10.9 mm. ***Head.*** Face yellow pruinose with shiny, black, medial vitta extending from oral margin to base of antenna; frons broad, about as long as broad at antenna, two-thirds as broad at vertex as at antenna, bare, with yellow pruinosity along posterior third; vertex triangular, longer than broad, shiny, with ocellar triangle black pilose; postocular border

yellow pruinose; postocular pile black; occipital pile yellow; male narrowly dichoptic; antenna black, black pilose, with length of segments roughly in a 2:2:1 ratio.

Thorax. Matte black; postpronotum yellow pilose; scutum yellow pilose, except with black pile posteromedially; scutellum yellow pilose anteriorly and black pilose posteriorly; postalar callus, proepimeron, posterior anepisternum yellow pilose; posterior katepisternum yellow pilose with broadly separated patches; anterior anepimeron yellow pilose; metasternum yellow pilose; postpronotum, anterior three-fourths of scutellum, broad posterior margin of anepisternum and dorso-posterior corner of katepisternum yellow pruinose; anepimeron usually shiny, rarely with weak pruinosity; scutum with two pairs of pruinose vittae: anterior pair long, running from anterior edge of scutum to transverse suture; posterior pair shorter and terminating before posterior edge; ventral calypter with long yellow pile.

Legs. Foreleg reddish-yellow, except basal four-fifths of femur and last three tarsomeres black; midleg reddish-yellow, except basal four-fifths of femur and last three tarsomeres black; hind leg reddish-yellow, except last two tarsomeres black; legs yellow pilose, except black pilose on last three tarsomeres; hind coxa yellow pruinose.

Wing. Hyaline; microtrichia absent from following areas: broad anterior margin of cell cua.

Abdomen. Tergites and sternites shiny to sub-shiny, black with yellow pruinose markings as follows: tergite 1 pruinose along posterior margin; tergite 2 with broad, interrupted, truncate medial band which meets a broad, uninterrupted posterior band in the posterolateral corners of tergite; tergite 3 with broad medial band, sometimes very narrowly interrupted, that joins with broad posterior band in two places, creating a medial diamond-shaped spot of no pruinosity; pattern on tergite 4 same as tergite 3; sternite 1 shiny; sternites 2 to 4 variable pruinose: ranging from almost completely pruinose, with a small region of non-pruinosity posteromedially to mostly pruinose, except with narrow anterior border and transverse subapical band shiny to dull black; sternites 6 to 8 pruinose; pile of abdomen yellow.

Male genitalia. Surstylus elongated, about two and a half times as long as broad, apex acute, directed ventrally; pile on dorsal surface of surstylus, increasing in length posteriorly; minute spines on ventral surface and apical three-fourths of lateral inner and outer surface; basal fourth of the ventral surface of the surstylus produced into a lobe directed ventrally, with minute pubescence on ventral and lateral inner surface; cerci rounded, with invagination on posterior border; aedeagus as in Fig. 2B.

Female. Similar to male except normal sexual dimorphism.

Distribution. U.S.A.: Washington, Oregon, California, Idaho, and Montana. Canada: Alberta and British Columbia (Fig. 23). Extends south from southern British Columbia, as well as the southeastern corner of Alberta, through the coastal and mountainous areas of Washington state, through Oregon and into the Sierra Nevada and midcoastal regions of California. Also known from forested regions of northern Idaho and western Montana.

Biology. Collected visiting flowers of *Vaccinium* L. sp., *Phacelia* Juss. sp., *Ceanothus* L. sp. and *Berberis aquifolium* Pursh. Recorded flying late April through late July, with one outlier in late August.

Remarks. *Sphecomyia brevicornis* shows intraspecific variation on sternites 2 to 4. Northern specimens (i.e. Washington, British Columbia, Idaho, Montana) possess larger non-pruinose, shiny areas on these sternites (Fig. 21G). On Californian specimens these sternites are more pruinose (Fig. 21H). In Oregon there are apparent intermediates of the two states. Californian specimens can be, but are not always, weakly pruinose on the anepimeron, as opposed to the shiny anepimeron found in most. No other morphological characters to distinguish between the two populations were found. Two barcodes for *S. brevicornis* were recovered. One from an Alberta specimen and one from a California specimen. The two were 1.3% different, however, neither barcode was complete with the Albertan one missing data at both ends of the sequence and the Californian one missing the middle B fragment. Additional and complete sequences of both the northern and southern morphotypes of *S. brevicornis* are needed to determine whether a gradient exists or whether two discrete clusters are resolved.

Sphecomyia columbiana Vockeroth, 1965

Figs 2C, 10A, 11A, 12A, 14A, 22C, 26

Sphecomyia columbiana Vockeroth 1965: 86 – Weisman 1965: 268, 1966: 194; Telford 1975: 21. Type locality: 32 miles southwest Terrace, British Columbia, Canada. [CNC]

Diagnosis. It can be confused with *S. cryptica* sp. n., *S. dyari*, *S. hoguei* sp. n., *S. oraria* sp. n., and *S. pattonii* but is distinguished by a tergite 1 densely pruinose only in the posterior corners.

Redescription. Male. Body length: 13.2–14.3 mm. Wing length: 9.9–10.5 mm. ***Head.*** Face yellow pruinose with shiny, black, medial vitta extending from oral margin to base of antenna; frons broad, about as long as broad at antenna, two-thirds as broad at vertex as at antenna, bare, with silver pruinosity along posterior half; vertex triangular, longer than broad, shiny, with ocellar triangle black pilose; postocular border yellow pruinose; postocular pile black; occipital pile yellow; male narrowly dichoptic; antenna black, black pilose, with length of segments roughly in a 3:3:2 ratio.

Thorax. Shiny black; postpronotum yellow pilose with occasional black pile; scutum and scutellum mostly black pilose with occasional yellow pile; postalar callus mixed black and yellow pilose; proepimeron yellow pilose; anepisternum yellow pilose posteriorly; posterior katepisternum yellow pilose with broadly separated patches; anterior anepimeron yellow pilose; metasternum yellow pilose; postpronotum, anterior eighth of scutellum, broad posterior margin of anepisternum and dorso-posterior corner of katepisternum yellow pruinose; area between postpronota weakly silver pruinose, except shiny medially; anepimeron shiny; scutum without pruinose vittae; ventral calypter with long yellow pile.

Legs. Foreleg black, except extreme apex of femur and anterior fourth of tibia reddish-yellow; fore tarsi slightly broadened; midleg reddish-yellow, except basal four-fifths of femur and last two tarsomeres black; hind leg reddish-yellow, except basal

four-fifths of femur and last two tarsomeres black; legs yellow pilose, except black pilose on fore tibia, fore tarsi, extreme apex of fore femur, and last two mid and hind tarsomeres; hind coxa silver pruinose.

Wing. Hyaline; microtrichia absent from following areas: cell bc; basal sixth of cell c; basal fourth of cell sc; cell r_1 from base almost to crossvein r-m; broad basal portion of cell br (before origin of M) and about basal two-fifths of narrower portion of this cell (caudad of spurious vein only); cell bm, except apex and narrow anterior and posterior margins of about apical fourth; broad anterior margin of cell cua; narrow, elongate, oval area proximal to vein A_1.

Abdomen. Tergites and sternites shiny to sub-shiny, black with yellow pruinose markings as follows: tergite 1 pruinose in posterolateral corners; tergite 2 with broad, interrupted, truncate medial band which meets a narrow, uninterrupted posterior band in the posterolateral corners of tergite; tergite 3 with similar medial band, but more narrowly interrupted; pattern on tergite 4 same as tergite 3, except medial band very narrowly or incompletely interrupted; sternite 1 shiny; sternites 2 to 4 mostly pruinose, except with narrow anterior border and transverse subapical band shiny to dull black; sternites 6 to 8 pruinose; pile of abdomen yellow, except with some black pile present on posterior halves of tergites 3 and 4 and on postabdomen.

Male genitalia. Surstylus not elongated, about as long as broad, curving downward ventrally; pile on anterolateral outer surface of surstylus; minute spines on ventral surface and apical half of interior lateral surface; basal fourth of the ventral surface of the surstylus produced into a lobe directed posteroventrally, with minute pubescence on ventral and lateral inner surface; cerci rounded, with no invagination on posterior border; aedeagus as in Fig. 2C.

Female. Similar to male except normal sexual dimorphism.

Distribution. Canada: British Columbia. U.S.A.: Washington (Fig. 26). Known from two close localities on the central coast of British Columbia and several clustered localities in southeastern Washington.

Biology. Collected visiting flowers of *Heracleum maximum* W. Bartram. Recorded flying April through June.

***Sphecomyia cryptica* Moran sp. n.**
http://zoobank.org/E96D3388-CEDE-4BB9-84A7-6F6ACEF800C7
Figs 2D, 7C, 8C, 9C, 15A, 21A, 22E, 25

Sphecomyia pattonii of authors Cole and Lovett 1921:293, not Williston 1882. Misidentification.

Type locality. U.S.A.: Oregon: Klamath County, Lake of the Woods, 42.36056, –122.205, 1500 m.

Types. ***Holotype*** male, pinned. Original label: "Crater Lake // Nat. Park" "A. L. Lovett // Coll *8 22*" "CNC47005". [1♂, CNC47005, CNC]

Paratypes: U.S.A., California: Del Norte Co., Darlingtonia, HWY 199, Six Rivers National Forest, 41.838611, –123.946111, 120 m, F.C. Thompson, 1.vi.2009, USNM_ENT01261991; USNM_ENT01261992; USNM_ENT01261993 (3♂, USNM); M. Hauser, 1.vi.2009, KMM0891; KMM0892 (2♂, CSCA). Oregon: 12–15 miles east of Ashland, Dead Indian Road, 42.2695, –122.4388, 1371 to 1493 m, H.A. Scullen, 17.vii.1930, KMM0805 (1♀, WIRC); Anna Creek, 42.9253, –122.1727, A.L. Lovett, 22.viii, CNC47006 (1♂, CNC); Crater Lake National Park, 42.8684, –122.1685, 2133 m, E.C. Van Dyke, 17.vii.1922, KMM0913; KMM0915 (2♀, CAS); A.L. Lovett, 22.viii, CNC47004; (1♂, CNC); KMM0903; KMM0904 (2♂, AMNH); D.C. Lowrie, 21.vii.1951, USNM01261990 (1♂, USNM); KMM0902 (1♀, WSU); E.C. Van Dyke, 14.vii.1934, KMM0914 (1♂, CAS); Douglas Co., Diamond Lake, 43.1699, –122.1681, E.C. Van Dyke, 16.vii.1934, KMM0916 (1♂, CAS); Jackson Co., 1.5 miles north Mount Ashland Ski Bowl, 42.1058, –122.6994, P. Rude, 4.vii.1970, EMEC371299 (1♂, EMEC); Jackson Co., Mount Ashland, 42.08, –122.7175, 2073 m, P. Rude, 26.vii.1966, EMEC371298; EMEC371348 (2♀, EMEC); Klamath Co., Crescent Lake, 43.5084, –121.9685, E.R. Jaycox, 4.vii.1952, CNC143004 (1♀, CNC); Klamath Co., Klamath Falls, Coary Ranch, 42.225, –121.78111, *Prunus demissa*, J. Schuh, 12.vi.1964, USNM1028902 (1♂, USNM); Klamath Co., Lake of the Woods, 42.3606, –122.205, E.C. Van Dyke, 10.vii.1934, KMM0906; KMM0907; KMM0908; KMM0909; KMM0910; KMM0911; KMM0912; KMM0917 (7♂,1♀, CAS); 42.360561, –122.205000, 1508 m, H.A. Scullen, 18.vii.1930, KMM0905 (1♂, WIRC); Klamath Co., Pelican Butte Road, 42.4633, –122.1103, P.H. Arnaud Jr., 29.vii.1967, USNM1071333 (1♂, USNM); Linn Co., Hoodoo Ski Bowl, 44.4072, –121.8719, 1402 m, P.A. Opler, 25.vii.1966, EMEC371347; EMEC371349; EMEC371350 (1♂,2♀, EMEC); Linn Co., Marion Forks, 44.6155, –121.9468, R.L. Fischner, 30.vi.1962, USNM01261994 (1♀, USNM); Mount Hood, Cloud Cap, 45.402875, –121.654162, 1520 m, M.C. Lane, 17.vii.1933, KMM0793; KMM0794 (2♂, WIRC); Mount Hood, 45.5389 -121.5681, 1524 m, M.C. Lane, 21.vi.1925, KMM0798 (1♂, WIRC); G.P. Englekardt, viii, USNM1028877; USNM1028911 (1♂,1♀, USNM); Mount Jefferson, 44.67429, –121.7990, subalpine regions, J.C. Bridwell, 20.vii.1907, CNC47015 (1♀, CNC); Timberline near Government Camp, Mount Hood, 45.3309, –121.7107, E.C. Van Dyke, 28.vii.1937, KMM0841; KMM0842 (2♀, CAS); Vidae Falls, Crater Lake National Park, 42.8844, –122.09970, B.V. Peterson, 10.vii.1968, CNC47016 (1♀, CNC).

Diagnosis. Species similar to *S. columbiana*, *S. dyari*, *S. hoguei* sp. n., *S. oraria* sp. n., and *S. pattonii* but can be distinguished by the following characters: tergite 1 with uninterrupted, pruinose band along posterior margin; scutellum mixed black and yellow pilose; ventral calypter with long yellow pile; sternites 2 to 4 almost completely pruinose, with a triangular region of non-pruinosity posteromedially.

Description. Male. Body length: 11.9–14.2 mm. Wing length: 8.9–10.7 mm. ***Head.*** Face yellow pruinose with shiny, black, medial vitta extending from oral margin to base of antenna; frons broad, about as long as broad at antenna, two-thirds as broad at vertex as at antenna, bare, with yellow pruinosity along posterior third; vertex tri-

angular, longer than broad, shiny, with ocellar triangle black pilose; postocular border yellow pruinose; postocular pile black; occipital pile yellow; male narrowly dichoptic; antenna black, black pilose, length of segments roughly in a 3:3:2 ratio.

Thorax. Sub-shiny black; postpronotum yellow pilose; scutum yellow pilose, except with black pile posteromedially; scutellum mostly yellow pilose with occasional black pile; postalar callus, proepimeron, posterior anepisternum yellow pilose; posterior katepisternum yellow pilose with broadly separated patches; anterior anepimeron yellow pilose; metasternum yellow pilose; postpronotum, anterior fourth of scutellum, broad posterior margin of anepisternum and dorso-posterior corner of katepisternum yellow pruinose; area between postpronota weakly yellow pruinose, except shiny medially; anepimeron shiny; scutum without pruinose vittae; ventral calypter with long yellow pile.

Legs. Foreleg black, except extreme apex of femur and anterior third of tibia reddish-yellow; fore tarsi slightly broadened; midleg reddish-yellow, except last two tarsomeres black; hind leg reddish-yellow, except last two tarsomeres black; legs yellow pilose, except, fore tibia, fore tarsi, extreme apex of fore femur and last two mid and hind tarsomeres black pilose; hind coxa yellow pruinose.

Wing. Hyaline; microtrichia absent from following areas: cell bc; cell r_1 from base to about halfway to crossvein r-m; broad basal portion of cell br (before origin of M) and about basal two-fifths of narrower portion of this cell (caudad of spurious vein only); cell bm, except apex and narrow anterior and posterior margins of about apical fourth; broad anterior margin of cell cua; narrow, elongate, oval area proximal to vein A_1.

Abdomen. Tergites and sternites shiny to sub-shiny, black with yellow pruinose markings as follows: tergite 1 pruinose along posterior margin; tergite 2 with broad, interrupted, truncate medial band which meets a narrow, uninterrupted posterior band in the posterolateral corners of tergite; tergite 3 with similar medial band, but more narrowly interrupted; pattern on tergite 4 same as tergite 3 except medial band very narrowly or incompletely interrupted; sternite 1 shiny; sternites 2 to 4 almost completely pruinose, with a triangular region of non-pruinosity posteromedially; sternites 6 to 8 pruinose; pile of abdomen yellow, except sometimes with scattered black pile present on postabdomen.

Male genitalia. Surstylus elongated, about twice as long as broad, curving upward dorsally; pile on dorsal surface of surstylus, increasing in length posteriorly; minute spines on ventral surface, with apical three-fourths of lateral inter surface also with spines; basal fourth of the ventral surface of the surstylus produced into a lobe directed anteriorly, with no minute pubescence present; cerci rounded, with invagination on posterior border; aedeagus as in Fig. 2D.

Female. Similar to male except normal sexual dimorphism.

Distribution. U.S.A.: Oregon (Fig. 25). Restricted to the Oregon portion of the Cascade Range.

Etymology. The specific epithet is derived from the Greek *kryptos* (Brown 1956: 241), which means hidden or secret and references the difficulty of distinguishing this species from *S. dyari* and *S. pattonii*.

Biology. Cole and Lovett (1921) misidentified specimens Lovett collected as *S. pattonii*. Lovett noted he observed them "entirely in the forenoon, occurring just at the edge of clearings and flying swiftly, close to the ground, resting occasionally in low growing shrubbery at the very edge of dense forests". They have been collected visiting flowers of *Prunus virginiana* var. *demissa* (Nutt. ex Torr. and A. Gray) Torr. A specimen collected by Bridwell notes it was collected in the sup-alpine region. Recorded flying June through August.

Sphecomyia dyari Shannon, 1925

Figs 2E, 7A, 8A, 9A, 21B, 25

Sphecomyia dyari Shannon 1925: 43 – Vockeroth 1965: 86; Stone et al. 1965: 612; Weisman 1965: 266, 1966a: 53, 1966b :196; Cole and Schlinger 1969: 331; Telford 1975: 21.

Type locality. Gold Lake Camp, Plumas County, California. [USNM]

Diagnosis. Can be confused with *S. columbiana*, *S. cryptica* sp. n., *S. hoguei* sp. n., *S. oraria* sp. n., and *S. pattonii* but can be distinguished by the following characters: Tergite 1 with uninterrupted, pruinose band along posterior margin. Scutellum mixed black and yellow pilose. Ventral calypter with long yellow pile. Sternites 2 to 4 with a posteromedial, triangular region of non-pruinosity on sternites 2 to 4 that is smaller on ensuing sternites. The species can only be distinguished from *S. hoguei* sp. n. by male genitalia in which the narrowest part of the surstylus is about one-fourth the width of base.

Redescription. Male. Body length: 11.2–14.4 mm. Wing length: 9.1–10.6 mm. ***Head.*** Face yellow pruinose with shiny, black, medial vitta extending from oral margin to base of antenna; frons broad, about as long as broad at antenna, two-thirds as broad at vertex as at antenna, bare, with yellow pruinosity along posterior three-fourths; vertex triangular, longer than broad, shiny, with ocellar triangle black pilose; postocular border yellow pruinose; postocular and occipital pile yellow; male narrowly dichoptic; antenna black, black pilose, length of segments roughly in a 3:3:2 ratio.

Thorax. Copper shine; postpronotum, scutum and scutellum yellow pilose, except scutum with black pile posteromedially; postalar callus, proepimeron, posterior anepisternum yellow pilose; posterior katepisternum yellow pilose with broadly separated patches; anterior anepimeron yellow pilose; metasternum yellow pilose; postpronotum, anterior fourth of scutellum, broad posterior margin of anepisternum and dorsoposterior corner of katepisternum yellow pruinose; area between postpronota weakly yellow pruinose, except shiny medially; anepimeron shiny; scutum without pruinose vittae; ventral calypter with long yellow pile.

Legs. Foreleg black, except extreme apex of femur and anterior third of tibia reddish-yellow; fore tarsi slightly broadened; midleg reddish-yellow, except basal four-fifths of femur and last two tarsomeres black; hind leg reddish-yellow, except basal four-fifths of femur and last two tarsomeres black; legs yellow pilose, except fore tibia,

fore tarsi, apex of fore femur and last two mid and hind tarsomeres black pilose; hind coxa yellow pruinose.

Wing. Hyaline; microtrichia absent from following areas: cell bc; cell r_1 from base to about halfway to crossvein r-m; broad basal portion of cell br (before origin of M) and about basal two-fifths of narrower portion of this cell (caudad of spurious vein only); cell bm, except apex and narrow anterior and posterior margins of about apical fourth; broad anterior margin of cell cua; narrow, elongate, oval area proximal to vein A_1.

Abdomen. Tergites and sternites shiny to sub-shiny, black with yellow pruinose markings as follows: tergite 1 pruinose along posterior margin; tergite 2 with broad, interrupted, truncate, medial band which meets a narrow, uninterrupted, posterior band in the posterolateral corners of tergite; tergite 3 with similar medial band, but more narrowly interrupted; pattern on tergite 4 same as tergite 3 except medial band very narrowly or incompletely interrupted; sternite 1 shiny; sternites 2 to 4 almost completely pruinose, with a triangular region of non-pruinosity posteromedially, with each ensuing region smaller; sternites 6 to 8 pruinose; abdominal pile yellow.

Male genitalia. Surstylus elongate, curving upward dorsally, more than three times as long as broad, about fourth the width of base at narrowest point; pile on dorsal surface of surstylus, symmetric in length; minute spines on ventral surface, with apical four-fifth of lateral inner surface also with spines; basal fourth of the ventral surface of the surstylus not produced into a lobe, but instead with slight invagination and no minute pubescence present; cerci with slight invagination on posterior border; aedeagus as in Fig. 2E.

Female. Similar to male except normal sexual dimorphism.

Distribution. U.S.A.: California, Oregon and Nevada (Fig. 25). Throughout the Sierra Nevada Mountains and Warner Mountains along with the portions of the Cascade Range, Klamath Mountains and the Northern Coast Ranges surrounding the Great Valley.

Biology. Species collected visiting flowers *Ceanothus cuneatus* (Hook.) Nutt. and recorded leafsitting on *Veratrum californicum* Durand. Recorded flying mid-May through mid-August.

Sphecomyia hoguei **Moran, sp. n.**

http://zoobank.org/75E07314-220F-40C8-AD72-A0FA726FED36
Figs 2F, 7B, 8B, 9B, 25

Type locality. U.S.A.: California: San Bernardino County, Summit of Mount Sorenson west of Running Springs, 34.237778, –117.155833, 1912 m.

Type. ***Holotype*** male, pinned. Original label: "USA: CA: San Bernardino Co. // Summit of Mount Sorenson // W of Running Springs; 1912 m // 31°14'16"N, 117°09'21"W // 8.vi.2003; J&A. Skevington" "CNC Diptera // # 110224" "*Sphecomyia // dyari //* [Handwritten] Det. J. Skevington, 2003", "Leg removed // for DNA // analysis". [1♂, CNC_Diptera110224, CNC]

***Paratypes*:** U.S.A., CALIFORNIA: Idyllwild, San Jacinto Mountains, 33.7456 -116.7161, J.W. MacSwain, 6.vii.1950, CNC143023 (1♂, CNC); 23.v.1940, CNC143019 (1♂, CNC); Los Angeles Co., Camp Baldy, 34.2689 -117.6286, 1981 m, R. DeNoble, 26.vi.1950, EMEC371314 (1♂, EMEC); R.C. Bechtel, 26.vi.1956, KMM0897 (1♂, CAS); R.W. Bushing, 26.vi.1956, KMM0896 (1♂, CAS); KMM0789 (1♂, SEMC); 7.vii.1958, KMM0898 (1♀, SEMC); San Bernardino Co., Forest Home, 34.0887. –116.9315, E.C. Van Dyke, 17.vi.1928, KMM0895 (1♂, CAS); San Bernardino Co., San Bernardino Mountains, Santa Ana River at Camp Metoche, 34.18, –116.88, 1710 m, J.N. Hogue, 8–9.vi.2013, LACM342617 (1♂, LACM); San Bernardino Co., Snow Crest Camp, 34.2546 -117.6337, A.A. Grigarick, 7.vii.1952, CNC143018 (1♀, CNC); D.E. Barcus, 7.vii.1952, KMM0899 (1♀, SEMC); E.M. Evans, 7.vii.1952, KMM0790 (1♀, SEMC); San Bernardino Co., Up Santa Ana River, 34.1465, –117.0563, J. & G. Sperry, 6.vi.1956, USNM1071433 (1♂, USNM); San Bernardino. Co., San Antonio Falls NE Mount Baldy P.O., 34.2719, –117.6342, *Rhamnus californica* in flower, J. Powell, 18.vi.1981, EMEC371306 (1♀, EMEC).

Diagnosis. It can be confused with *S. columbiana*, *S. cryptica* sp. n., *S. dyari*, *S. oraria* sp. n. and *S. pattonii* but can be distinguished by the following characters: tergite 1 with uninterrupted, pruinose band along posterior margin; scutellum mixed black and yellow pilose; ventral calypter with long yellow pile; sternites 2 to 4 with a posteromedial, triangular region of non-pruinosity on sternites 2 to 4 that is smaller on ensuing sternites. The species can only be distinguished from *S. hoguei* sp. n. by male genitalia in which the narrowest part of the surstylus is about one half the width of base.

Description. Male. Body length: 12.5–14.7 mm. Wing length: 8.8–10.5 mm. ***Head.*** Face yellow pruinose with shiny, black, medial vitta extending from oral margin to base of antenna; frons broad, about as long as broad at antenna, two-thirds as broad at vertex as at antenna, bare, with yellow pruinosity along posterior three-fourths; vertex triangular, longer than broad, shiny, with ocellar triangle black pilose; postocular border yellow pruinose; postocular and occipital pile yellow; male narrowly dichoptic; antenna black, black pilose, length of segments roughly in a 3:3:2 ratio.

Thorax. Copper shine; postpronotum, scutum and scutellum yellow pilose, except scutum with black pile posteromedially; postalar callus, proepimeron, posterior anepisternum yellow pilose; posterior katepisternum yellow pilose with broadly separated patches; anterior anepimeron yellow pilose; metasternum yellow pilose; postpronotum, anterior fourth of scutellum, broad posterior margin of anepisternum and dorsoposterior corner of katepisternum yellow pruinose; area between postpronota yellow pruinose, except shiny medially; anepimeron shiny; scutum without pruinose vittae; ventral calypter with long yellow pile.

Legs. Foreleg black, except extreme apex of femur and anterior third of tibia reddish-yellow; fore tarsi slightly broadened; midleg reddish-yellow, except basal four-fifths of femur and last two tarsomeres black; hind leg reddish-yellow, except basal four-fifths of femur and last two tarsomeres black; legs yellow pilose, except fore tibia, fore tarsi, apex of fore femur and last two mid and hind tarsomeres black pilose; hind coxa yellow pruinose.

Wing. Hyaline; microtrichia absent from following areas: cell bc; cell r_1 from base to about halfway to crossvein r-m; broad basal portion of cell br (before origin of M) and about basal two-fifths of narrower portion of this cell (caudad of spurious vein only); cell bm, except apex and narrow anterior and posterior margins of about apical fourth; broad anterior margin of cell cua; narrow, elongate, oval area proximal to vein A_1.

Abdomen. Tergites and sternites shiny to sub-shiny, black with yellow pruinose markings as follows: tergite 1 pruinose along posterior margin; tergite 2 with broad, interrupted, truncate medial band which meets a narrow, uninterrupted posterior band in the posterolateral corners of tergite; tergite 3 with similar medial band, but more narrowly interrupted; pattern on tergite 4 same as tergite 3 except medial band very narrowly or incompletely interrupted; sternite 1 shiny; sternites 2 to 4 almost completely pruinose, with a triangular region of non-pruinosity posteromedially, with each ensuing region smaller; sternites 6 to 8 pruinose; abdominal pile yellow.

Male genitalia. Surstylus elongated, curving upward dorsally, more than three times as long as broad, no less than half the width of base at narrowest point; pile on dorsal surface of surstylus, symmetric in length; minute spines on ventral surface, with apical four-fifths of lateral inner surface also with spines; basal fourth of the ventral surface of the surstylus not produced into a lobe, with no invagination or minute pubescence present; cerci with slight invagination on posterior border; aedeagus as in Fig. 2F.

Female. Similar to male except normal sexual dimorphism.

Distribution. U.S.A.: California (Fig. 25). Known from San Gabriel, San Bernardino, and San Jacinto mountains.

Biology. Collected visiting flowers of *Frangula californica* (Eschsch.) A. Gray. Recorded flying late May through early July.

Etymology. The specific epithet honors J. N. (Jim) Hogue who collected many of the specimens of *S. hoguei* sp. n., *S. interrupta* sp. n., and *S. sexfasciata* sp. n.

***Sphecomyia interrupta* Moran, sp. n.**
http://zoobank.org/8C026307-8B40-49C0-B213-6D5B6223E841
Figs 2G, 4A, 5A, 16C, 17C, 18C, 21F, 22B, 23

Type locality. U.S.A. California: San Bernardino Co., Summit of Heap's Peak west of Running Springs, 34.2347, –117.1397, 1957 m.

Types. ***Holotype*** male, pinned. Original label: "USA: CA: San Bernardino Co. // Summit of Heap's Peak W. // Of Running Springs; 1957 m // 34°14'05" N, 117°08'23" W // 25.v.2003; J. Skevington", "CNC DIPTERA // #110220", "*Sphecomyia // brevicornis //* [Handwritten] Det. J. Skevington, 2003", "Leg removed // for DNA // analysis". [1♂, CNC_DIPTERA110220, CNC]

***Paratypes*:** U.S.A., CALIFORNIA: Camp Angelus, 34.1461, –116.9825, white *Ceanothus*, A.L. Melander, 20.v.1947, KMM0900 (1♂, RMNH); San Bernardino Co., Mill Creek, 34.0972, –117.0289, 1828–1920 m, on *Ceanothus*, Timberlake, 30.v.1934, UCRC442807 (1♂, UCRC); San Bernardino Co., San Antonio Canyon,

34.160256, –117.678477, 1889–1950 m, J.N. Hogue, 20.vi.1968, LACM329893 (1♀, LACM).

Diagnosis. Species similar to *S. brevicornis* and *S. sexfasciata* sp. n. but can be distinguished by the following characters: scutum with two pairs of pruinose vittae; cell c completely microtrichose; antenna possessing a 3:3:2 ratio of segments; frons bare; anepimeron not pruinose; scutellum entirely pruinose; medial facial vitta interrupted by a macula of pruinosity on tubercle.

Description. Male. Body length: 12.5–14.0 mm. Wing length: 8.9–10.7 mm. ***Head.*** Face yellow pruinose with shiny, black, medial vitta extending from oral margin to base of antenna, except interrupted on facial tubercle by yellow pruinosity; frons broad, about as long as broad at antenna, two-thirds as broad at vertex as at antenna, bare, with yellow pruinosity along posterior half; vertex triangular, longer than broad, shiny, with ocellar triangle black pilose; postocular border yellow pruinose; postocular pile black; occipital pile yellow; male narrowly dichoptic; antenna black, black pilose, with length of segments roughly in a 3:3:2 ratio.

Thorax. Matte black; postpronotum yellow pilose; scutum yellow pilose, except with black pile posteromedially; scutellum, postalar callus, proepimeron, posterior anepisternum yellow pilose; posterior katepisternum yellow pilose with broadly separated patches; anterior anepimeron yellow pilose; metasternum yellow pilose; postpronotum, anterior three-fourths of scutellum, broad posterior margin of anepisternum and dorso-posterior corner of katepisternum yellow pruinose; anepimeron shiny; scutum with two pairs of pruinose vittae: anterior pair long, running from anterior edge of scutum to transverse suture; posterior pair shorter and terminating before posterior edge; ventral calypter with long yellow pile.

Legs. Foreleg reddish-yellow, except basal four-fifths of femur and last two tarsomeres black; midleg reddish-yellow, except basal four-fifths of femur and last two tarsomeres black; hind leg reddish-yellow, except last two tarsomeres black; legs yellow pilose, except black pilose on last three tarsomeres; hind coxa yellow pruinose.

Wing. Hyaline; microtrichia absent from following areas: cell bc; narrow anteromedial region of cell bm; broad anterior margin of cell cua.

Abdomen. Tergites and sternites shiny to sub-shiny, black with yellow pruinose markings as follows: tergite 1 pruinose along posterior margin; tergite 2 with broad, interrupted, truncate medial band which meets a broad, uninterrupted posterior band in the posterolateral corners of tergite; tergite 3 with broad medial band, sometimes very narrowly interrupted, that joins with broad posterior band in two places creating a medial diamond-shaped spot of no pruinosity; pattern on tergite 4 same as tergite 3; sternite 1 pruinose on posterior half; sternites 2 to 4 completely pruinose; sternites 6 to 8 pruinose; pile of abdomen yellow.

Male genitalia. Surstylus elongated, about two and a half times as long as broad, apex acute, with rounded curve, directed ventrally; pile on dorsal surface of surstylus, increasing in length posteriorly; minute spines on ventral surface and apical three-fourth of lateral inner and outer surface; basal fourth of the ventral surface of the surstylus produced into a conspicuous lobe which extends ventrally, with minute pu-

bescence on ventral and lateral inner surface; cerci rounded, with invagination on posterior border; aedeagus as in Fig. 2G.

Female. Medial, facial vittae not interrupted.

Distribution. U.S.A.: California (Fig. 23). Known only from the San Bernardino Mountains.

Biology. Collected visiting flowers of *Ceanothus* L. Recorded flying late May to late June.

Etymology. The specific epithet is derived from the Latin *interruptus* (Brown 1956: 441) which means broken apart, between, off, or asunder. It references that the medial facial vitta is interrupted on the tubercle by a macula of pruinosity.

***Sphecomyia metallica* (Bigot, 1882), stat. rev. and comb. n.**
Figs 2H, 4B, 16E, 17E, 18E, 26

Eurhinomallota metallica Bigot 1882: 78. Type Locality: ?California [see below] [UMO]
Brachymyia lupina Williston 1882a: 77. Type Locality: California. **Syn. nov.** [USNM]
Eurhinomallota lupina Williston 1882b: 330.
Criorhina lupina Williston 1886: 209 – Kertész 1910: 288; Curran 1925f: 157; Byers et al. 1962: 167; Nayar 1968: 297; Cole and Schlinger 1969: 330; Telford 1975: 20.

Diagnosis. *Sphecomyia metallica* is not easily confused with any other congeneric as it is the only species which is long pilose and also completely pruinose on the scutum and scutellum.

Redescription. Male. Body length: 9.2–13.2 mm. Wing length: 7.9–10.7 mm. ***Head.*** Face silver pruinose with shiny, black, medial vitta extending from oral margin to tubercle; frons broad, about as long as broad at antenna, as broad at vertex as at antenna, pale pilose and silver pruinose; vertex polygonal, slightly longer than broad, silver pruinose, with ocellar triangle pale pilose; postocular border silver; postocular and occipital pile pale; broadly dichoptic in male; antenna black, pale pilose, length of segments roughly in a 3:3:2 ratio.

Thorax. Black; long pilose; postpronotum, scutum, scutellum, postalar callus, proepimeron, posterior anepisternum pale pilose; posterior katepisternum pale pilose with broadly separated patches; anterior anepimeron pale pilose; metasternum pale pilose; postpronotum, mesonotum, broad posterior margin of anepisternum, dorsoposterior corner of katepisternum and anepimeron silver pruinose.

Legs. Foreleg black, except extreme apex of femur and anterior third of tibia reddish-yellow; mid and hind leg similar; tarsi not modified; leg pale pilose; hind coxa silver pruinose.

Wing. Hyaline; wing completely microtrichose.

Abdomen. Tergites and sternites shiny to sub-shiny, black with silver pruinosity as follows: tergite 1 completely silver pruinose; tergite 2 weakly silver pruinose; tergite 3 weakly silver pruinose along margins with thin, interrupted medial band;

tergite 4 as tergite 3; sternites 1 to 4 completely silver pruinose; pile of abdomen long, pale.

Male genitalia. Surstylus elongated, about 2½ times as long as broad, apex acute, with rounded curve, directed ventrally; pile on dorsal surface of surstylus, increasing in length posteriorly; minute spines on ventral surface and apical three-fourth of lateral inner and outer surface; basal fourth of the ventral surface of the surstylus produced into a lobe directed ventrally, with minute pubescence on ventral and lateral inner surface; cerci rounded, with conspicuous invagination on posterior border; aedeagus as in Fig. 2H.

Female. Similar to male except normal sexual dimorphism and as follows: medial facial vittae extends past tubercle to terminate just below antenna.

Distribution. U.S.A.: California, Oregon (Fig. 26). Mostly restricted to California, with a short extension into coastal Oregon.

Biology. Associated with lowland *Arctostaphylos* Adans. sp., more commonly known as manzanitas or bearberries. The plant ranges from small shrubs to trees of over 6 m. It has small, clustered, bell-shaped, pink or white flowers. Also collected on flowers of *Ribes sanguineum* Pursh and *Ribes menziesii* Pursh. Due to their unusual flight period of December through mid-April, more research is necessary to reveal the true distribution of the species.

Remarks. Although the type locality is listed as Mexico, the authors believe that the type is from current-day California as it was collected prior to 1848 when the state was still part of Mexico.

Contrary to the previous treatment, *Eurhinomallota metallica* Bigot, 1882 is senior to *Brachymyia lupina* Williston, 1882. Bigot's name was published in the bimonthly Bulletin de la Société entomologique de France in March of 1882. Williston's name was published in the April 1882 issue of the Canadian Entomologist. The improper treatment arose because the Bulletin itself was obscure until recently, with the Annales de la Société entomologique de France, the annually published compilation, taken as the date of publication for many species.

The combination of *Eurhinomallota* with *Sphecomyia* is supported by the type species' possession of all characters used to distinguish *Sphecomyia* from other Criorhinina. This decision is further supported by molecular evidence showing a close relationship with *Sphecomyia*, i.e., the present COI gene tree (Fig. 27) and a multi-gene molecular phylogeny of the Criorhinina which will be presented in an upcoming paper. It is the authors opinion that combination with *Sphecomyia*, as opposed to resurrecting the concept as a monotypic genus, serves to emphasize its relationship with the group.

Sphecomyia oraria Moran, sp. n.

http://zoobank.org/36910837-6671-464C-B22A-5C0D95EAEDAC
Figs 2I, 7E, 8E, 9E, 15B, 20A, 21C, 25

Type locality. U.S.A.: California: Marin County, 2 miles SE Inverness, Inverness Ridge, 38.1014, –122.8869.

Types. ***Holotype*** male, pinned. Original label: "CALIF: Marin Co., // 2 mi SE Inverness, // Inverness Ridge, // at light, May 15, // 1970, J. A. Powell" "Univ. Calif. // Insect Survey // Specimen # // 111082" "UC Berkley // EMEC // 371304 // [BARCODE]". [1♂, EMEC371304, EMEC].

Paratypes**:** U.S.A.: California: Humboldt Co., Blocksburg, 40.2756 -123.6364, B.P. Bliven, 30.v.1937, KMM0894 (1♀, CAS); Marin Co., 2 mi. SE Inverness, Inverness Ridge, 38.1014, –122.8870, 243–316 m, H. Ewing, 7.v.1971, EMEC371305 (1♂, EMEC); Marin Co., Lily Pond, Alpine Lake, 37.9538, –122.6349, 457 m, D.D. Munroe, 10.v–4.vi.1970, CNC47070 (1♀, CNC); Mendocino Co., NCCRP, 3 mi. N. Branscomb, 39.6464 -123.4470, 427 m, C. Strong, 21–23.v.1982, EMEC371315 (1♀, EMEC); San Luis Obispo Co., Atascadero, 35.4883 -120.6703, J. LeCroy, 4.v.1986, LACM329903 (1♀, LACM); Santa Clara Co., Creek along Sandborn road, 2.7 km SE Congree-Springs road, 37.2347, –122.0589, 440 m, P.H. Arnaud, Jr., 14.iv.1974, USNM1028896 (1♂, USNM); Sonoma Co., Plantation, 38.5903 -123.3103, D. Burdick, 1.v.1958, INHS776993 (1♂, INHS); Sonoma Co., Stillwater Cove, 38.5424, –123.2888, E.I. Schlinger, 23.v.1954, KMM0893 (1♂, CAS); USNM1028841 (1♂, CNC); Walnut Creek, 37.9103, –122.0653, v, USNM1028837 (1♀, USNM).

Diagnosis. It can be confused with *S. columbiana*, *S. cryptica* sp. n., *S. dyari*, *S. hoguei* sp. n., and *S. pattonii* but can be distinguished by the following characters: tergite 1 with uninterrupted, pruinose band along posterior margin. Scutellum black pilose. Ventral calypter with long yellow pile. Sternites 2 to 4 mostly pruinose, with narrow anterior border and transverse subapical band shiny to dull black.

Description. Male. Body length: 11.1–14.6 mm. Wing length: 8.9–11.6 mm. ***Head.*** Face yellow pruinose with shiny, black, medial vitta extending from oral margin to base of antenna; frons broad, about as long as broad at antenna, two-thirds as broad at vertex as at antenna, bare, with yellow pruinosity along posterior half; vertex triangular, longer than broad, shiny, with ocellar triangle black pilose; postocular border yellow pruinose; postocular pile black; occipital pile yellow; male narrowly dichoptic; antenna black, black pilose, with length of segments roughly in a 3:3:2 ratio.

Thorax. Sub-shiny black; postpronotum yellow pilose with occasional black pile; scutum, scutellum and postalar callus mostly black pilose with occasional yellow pile; proepimeron and posterior anepisternum yellow pilose; posterior katepisternum yellow pilose with broadly separated patches; anterior anepimeron yellow pilose; metasternum yellow pilose; postpronotum, anterior fourth of scutellum, broad posterior margin of anepisternum and dorso-posterior corner of katepisternum yellow pruinose; area between postpronota yellow pruinose, except shiny medially; anepimeron shiny; scutum without pruinose vittae; ventral calypter with long yellow pile.

Legs. Foreleg black, except extreme apex of femur and anterior third of tibia reddish-yellow; fore tarsi slightly broadened; midleg reddish-yellow, except basal four-fifths of femur and last two tarsomeres black; hind leg reddish-yellow except last two tarsomeres black; legs yellow pilose, except fore tibia, fore tarsi, apex of fore femur and last two mid and hind tarsomeres black pilose; hind coxa yellow pruinose.

Wing. Hyaline; microtrichia absent from following areas: cell bc; cell r_1 from base to about halfway to crossvein r-m; broad basal portion of cell br (before origin of M) and about basal two-fifths of narrower portion of this cell (caudad of spurious vein only); cell bm, except apex and narrow anterior and posterior margins of about apical fourth; broad anterior margin of cell cua; narrow, elongate, oval area proximal to vein A_1.

Abdomen. Tergites and sternites shiny to sub-shiny, black with yellow pruinose markings as follows: tergite 1 pruinose along posterior margin; tergite 2 with broad, interrupted, narrowing, medial band which meets a narrow, uninterrupted posterior band in the posterolateral corners of tergite; tergite 3 with similar, but truncate, medial band, but more narrowly interrupted; pattern on tergite 4 same as tergite 3 except medial band very narrowly or incompletely interrupted; sternite 1 shiny; sternites 2 to 4 mostly pruinose, each with narrow anterior border and transverse subapical band shiny to dull black; sternites 6 to 8 pruinose; pile of abdomen yellow, except sometimes with scattered black pile present on postabdomen.

Male genitalia. Surstylus not elongated, about as long as broad, curving upward dorsally; pile on dorsal surface of surstylus, increasing in length posteriorly; minute spines on ventral surface, with apical half of lateral inner surface also with spines; basal fourth of the ventral surface of the surstylus produced into a lobe directed anteriorly, with minute pubescence on ventral and lateral inner surface; cerci rounded, with no invagination on posterior border; aedeagus as in Fig. 2I.

Female. Similar to male except normal sexual dimorphism.

Distribution. U.S.A.: California (Fig. 25). A lowland species spread throughout the California Coast Ranges.

Biology. Recorded flying late April through May.

Etymology. The specific epithet is derived from the Latin *orarius* (Brown 1956: 576), meaning 'of the coast'.

Sphecomyia pattonii Williston, 1882

Figs 2J, 7F, 8F, 9F, 11B, 20B, 25

Sphecomyia pattonii Williston 1882b: 328 – Kertész 1910: 349; Vockeroth 1965: 86; Stone et al. 1965: 613; Weisman 1965: 268, 1966a: 53, 1966b :194; Boyes and van Brink 1967: 432, 1970: 212; Cole and Schlinger 1969: 331; Telford 1975: 21; Hippa 1978: 15. **Type locality.** "Washington Territory". [USNM]

Calliprobola calorhina Bigot 1884: 353 – Williston 1887: 258. **Type locality.** "Washington Territory". [UMO]

Sphecomyia pattoni Williston 1886: 258 – Aldrich 1905: 404; Osburn 1908: 14; Shannon 1925: 43; Curran 1932: 8.

Diagnosis. Species similar to *S. columbiana*, *S. cryptica* sp. n., *S. dyari*, *S. hoguei* sp. n. and *S. oraria* sp. n. but can be distinguished by the following characters: tergite 1 with uninterrupted, pruinose band along posterior margin; scutellum black pilose; ventral

calypter with long black pile; sternites 2 to 4 mostly pruinose, with narrow anterior border and transverse subapical band shiny to dull black.

Redescription. Male. Body length: 12.1–16.0 mm. Wing length: 8.3–11.8 mm. ***Head.*** Face yellow pruinose with shiny, black, medial vitta extending from oral margin to base of antenna; frons broad, about as long as broad at antenna, two-thirds as broad at vertex as at antenna, bare, with yellow pruinosity along posterior fourth; vertex triangular, longer than broad, shiny, with ocellar triangle black pilose; postocular border yellow pruinose; postocular pile black, occipital pile yellow; male narrowly dichoptic; antenna black, black pilose, with length of segments roughly in a 3:3:2 ratio.

Thorax. Sub-shiny black; postpronotum yellow pilose with occasional black pile; scutum and scutellum mostly black pilose with occasional yellow pile; postalar callus mixed black and yellow pilose; proepimeron, posterior anepisternum yellow pilose; posterior katepisternum yellow pilose with broadly separated patches; anterior anepimeron yellow pilose; metasternum yellow pilose; postpronotum, anterior fourth of scutellum, broad posterior margin of anepisternum and dorso-posterior corner of katepisternum yellow pruinose; area between postpronota yellow pruinose, except shiny medially; anepimeron shiny; scutum without pruinose vittae; ventral calypter with long black pile.

Legs. Foreleg black, except extreme apex of femur and anterior third of tibia reddish-yellow; fore tarsi slightly broadened; midleg reddish-yellow, except basal four-fifths of femur and last two tarsomeres black; hind leg reddish-yellow except last two tarsomeres black; legs yellow pilose, except fore tibia, fore tarsi, apex of fore femur and last two mid and hind tarsomeres black pilose; hind coxa yellow pruinose.

Wing. Hyaline; microtrichia absent from following areas: cell bc; cell r_1 from base almost to crossvein r-m; broad basal portion of cell br (before origin of M) and about basal two-fifths of narrower portion of this cell (caudad of spurious vein only); cell bm except apex and narrow anterior and posterior margins of about apical fourth; broad anterior margin of cell cua; narrow, elongate, oval area proximal to vein A_1.

Abdomen. Tergites and sternites shiny to sub-shiny, black with yellow pruinose markings as follows: tergite 1 pruinose along posterior margin; tergite 2 with broad, interrupted, narrowing medial band which meets a narrow, uninterrupted posterior band in the posterolateral corners of tergite; tergite 3 with similar, but truncate, medial band more narrowly interrupted; pattern on tergite 4 same as tergite 3 except medial band very narrowly or incompletely interrupted; sternite 1 shiny; sternites 2 to 4 mostly pruinose, each with narrow anterior border and transverse subapical band shiny to dull black; sternites 6 to 8 pruinose; pile of abdomen yellow, except sometimes with scattered black pile present on postabdomen.

Male genitalia. Surstylus elongated, about 1½ times as long as broad, curving upward dorsally; pile on dorsal surface of surstylus, increasing in length posteriorly; minute spines on ventral surface of surstylus, with apical three-fourths of lateral inner surface also with spines; basal fourth of the ventral surface of the surstylus produced into a lobe directed anteriorly, with minute pubescence on ventral and lateral inner surface; cerci rounded, with no invagination on posterior border; aedeagus as in Fig. 2J.

Female. Similar to male except normal sexual dimorphism.

Distribution. U.S.A.: Washington, Oregon, Idaho, Montana. Canada: British Columbia (Fig. 25). Widespread throughout coastal and mountainous areas of Washington state except seemingly absent from the Columbia basin. Extends into coastal and forested parts of northeastern Oregon. Extends north into forested coastal and inland areas of British Columbia. Also known from forests of northern Idaho and western Montana.

Biology. The authors collected this species visiting *Rubus* L. sp. on a forested slope near a river. Also collected visiting flowers of *Heracleum lanatum* Michx. Known hilltopper. Recorded flying late April through mid-August, with one outlier from mid-October.

Sphecomyia pseudosphecomima **Moran, sp. n.**
http://zoobank.org/3371F4A6-3010-416D-9260-EA89EB01DE69
Figs 10C, 12C, 26

Type locality. U.S.A.: California: Tulure Co., Ash Mountain Headquarters, 36.4868, –118.8398, 518 m.

Types. ***Holotype*** female, pinned. Original label: CAL: Tulare Co. // Ash Mt. HQ, 1700' // IV-28-1979 // J. Powell, coll." "EMEC // 371308 // [BARCODE]". [1♀, EMEC371308, EMEC]

Paratypes**:** U.S.A.: California: Kern Co., Glennville, 35.7236, –118.7021, E.G. Linsley, J.W. MacSwain, R.F. Smith, 24.iv.1949, CNC91444 (1♀, CNC); Yosemite National Park, 37.7399, –119.5911, E.C. Van Dyke, 16.v.1921, USNM1028990 (1♀, USNM).

Diagnosis. Species similar to *S. aino* or *S. tsherepanovi* but can be distinguished by the following characters: cell c bare on basal third; ocellar triangle pale pilose; silver-yellow pruinose.

Description. Female. Body length: 9.9 –12.7 mm. Wing length: 7.7–7.9 mm. ***Head.*** Face silver-yellow pruinose with shiny, black, medial vitta extending from oral margin to base of antenna; frons black pilose posteriorly, silver-yellow pruinose on lateral margins; postocular border silver-yellow pruinose; postocular and occipital pile pale; antenna black, black pilose, with length of segments roughly in a 3:3:2 ratio.

Thorax. Sub-shiny black; postpronotum, scutum, scutellum, postalar callus, proepimeron, posterior anepisternum pale pilose; posterior katepisternum pale pilose with broadly separated patches; anterior anepimeron pale pilose; metasternum pale pilose; postpronotum, anterior eighth of scutellum, broad posterior margin of anepisternum and dorso-posterior corner of katepisternum silver-yellow pruinose; area between postpronota weakly silver-yellow pruinose, except shiny medially; anepimeron shiny; scutum without pruinose vittae; ventral calypter with long yellow pile.

Legs. Foreleg black except extreme apex of femur; midleg reddish-yellow, except last two tarsomeres black; hind leg reddish-yellow except last two tarsomeres black; all of fore tibia and tarsus black pilose, remainder of leg pale pilose.

Wing. Hyaline; microtrichia absent from following areas: cell bc; basal third of cell c; basal fourth of cell sc; cell r_1 from base almost to crossvein r-m; broad basal portion of cell br (before origin of M) and about basal two-fifths of narrower portion of this cell (caudad of spurious vein only); cell bm except apex and narrow anterior and posterior margins of about apical fourth; broad anterior margin of cell cua; narrow, elongate, oval area proximal to vein A_1.

Abdomen. Tergites and sternites shiny to sub-shiny, black with silver-yellow pruinosity as follows: tergite 1 pruinose posteriorly; tergite 2 with thin, interrupted, medial band which curves posteriorly to reach the posterolateral corners; tergite 3 with thin, interrupted, medial band which does not curve anteriorly; tergite 4 with similar but thinner band; sternite 1 shiny; sternites 2 to 4 pruinose, with indistinct spot of non-pruinosity posteromedially; pile of abdomen pale.

Male. Unknown.

Distribution. U.S.A.: California (Fig. 26). Known from three localities in the Sierra Nevada Range.

Biology. Recorded flying late April through mid-May.

Etymology. The specific epithet is derived from the Greek *pseudo* (Brown 1956: 652) meaning false and *sphex* meaning wasp (Brown 1956: 652) and the latin *mima* (Brown 1956: 652) for mimic. The epithet referencing that it is one of the few non-wasp mimics of *Sphecomyia*.

***Sphecomyia sexfasciata* Moran, sp. n.**
http://zoobank.org/B7776D23-4486-45D1-AB1E-A34A0CDD75C4
Figs 2K, 16B, 17B, 18B, 23

Type locality. U.S.A: California**,** Ventura Co., Ventura Mountains, Pine Mountain Creek, just south of Reyes Creek Campground, 34.677, –119.308, 1190 m.

Type. ***Holotype*** male, pinned. Original label: "USA: California: Ventura Co. // Ventura Mountains, Pine Mountain // creek just S. of Reyes Cr. Cmpgrd. // 34.677° N, –119.308° W, elev 1190 m // at Prunus virginiana var. demisa // 29 April–1 May 2016 // J. N. Hogue, notes JNH# 526" "LACM ENT 342251". [1♂, LACMENT342251, LACM]

Paratypes**:** U.S.A.: California, Arroyo Seco, 34.118483, –118.191733, C.D. Michener, 27.i.1935, CNC46969 (1♂, CNC); Monterey Co., Highway. 1, roadside canyon 3.5 km N Lucia, 36.0589, –121.5875, K.C. Holston, 15.v.2001, KMM0901 (1♀, CSCA); Riverside Co., Morongo Valley, 34.0451, –116.5668, W. Laidlaw, 28.iv.1972, JSS45129 (1♀, CAS); Riverside Co., Riverside, 33.9533, –117.3919, *Salix lasiolepis*, 26.ii.1933, UCRC428629; UCRC428631 (1♂,1♀, UCRC); San Bernardino Co., Big Morongo Canyon Preserve, 34.0507, –116.5694, J.H. Skevington, K. Moran, 25.iv.2016, CNC517072 (1♀, CNC); Ventura Co., Ventura Mountains, Pine Mountain Creek, just South of Reyes Creek Campground, 34.677, –119.308, 1190 m, *Prunus virginiana* var. *demisa*, A.M. Haberkern, 30.iv.2016, LACMENT342306 (1♂, USNM); J.N. Hogue, 29.iv–1.v.2016, LACMENT342252 (1♂, LACM).

Diagnosis. Species similar to *S. brevicornis* and *S. interrupta* sp. n. but can be distinguished by the following characters: scutum with three pairs of pruinose vittae; cell c completely microtrichose; antenna possessing a 3:3:2 ratio of segments; frons pilose; anepimeron pruinose; anterior three-fourth of scutellum pruinose; medial facial vitta not interrupted by a macula of pruinosity on tubercle.

Description. Male. Body length: 12.3–12.6 mm. Wing length: 8.9–9.6 mm. ***Head.*** Face yellow pruinose with shiny, black, medial vitta extending from oral margin to base of antenna; frons broad, about as long as broad at antenna, two-thirds as broad at vertex as at antenna, sparsely yellow pilose, with yellow pruinosity along posterior fourth; vertex triangular, longer than broad, shiny, with ocellar triangle black pilose; postocular border yellow pruinose; postocular pile black; occipital pile yellow; male narrowly dichoptic; antenna black, black pilose, length of segments roughly in a 3:3:2 ratio.

Thorax. Matte black; postpronotum yellow pilose; scutum yellow pilose, except with black pile posteromedially; scutellum, postalar callus, proepimeron, posterior anepisternum yellow pilose; posterior katepisternum yellow pilose with broadly separated patches; anterior anepimeron yellow pilose; metasternum yellow pilose; postpronotum, scutellum, broad posterior margin of anepisternum and dorso-posterior corner of katepisternum yellow pruinose; anepimeron yellow pruinose anteriorly; scutum with three pairs of pruinose vittae, anterior pair long running from anterior edge of scutum to transverse suture, posterior pair shorter and terminating before posterior edge and a small medial pair along the lateral margins of the scutum; ventral calypter with long yellow pile.

Legs. Fore femur, except for extreme apex, along with last two tarsi black; rest of leg yellow; midleg with femur except extreme apex, and last two tarsomeres, black; rest of leg reddish-yellow; hind leg reddish-yellow except last two tarsomeres black; legs yellow pilose, except black pilose on last three tarsomeres;

Wing. Hyaline; microtrichia absent from following areas: broad anterior margin of cell cua.

Abdomen. Tergites and sternites shiny to sub-shiny, black with yellow pruinose markings as follows: tergite 1 pruinose along posterior margin; tergite 2 with broad, interrupted, truncate medial band which meets a broad, uninterrupted posterior band in the posterolateral corners of tergite; tergite 3 with broad medial band, sometimes very narrowly interrupted, that joins with broad posterior band in two places creating a medial diamond-shaped spot of no pruinosity; pattern on tergite 4 same as tergite 3; sternites 1 to 4 completely pruinose; sternites 6 to 8 pruinose; pile of abdomen yellow.

Male genitalia. Surstylus elongated, about 2½ times as long as broad, apex acute, directed ventrally, with abrupt curve; pile on dorsal surface of surstylus, increasing in length posteriorly; minute spines on ventral surface and apical three-fourth of lateral inner and outer surface; basal fourth of the ventral surface of the surstylus produced into a lobe directed ventrally, with minute pubescence on ventral and lateral inner surface; cerci rounded, with invagination on posterior border; aedeagus as in Fig. 2K.

Female. Similar to male except normal sexual dimorphism.

Distribution. U.S.A.: California (Fig. 23). Lowland chaparral in southern California.

Biology. Collected visiting flowers of *Salix lasiolepis* Benth. and *Prunus virginiana* var. *demisa* (Nutt. ex Torr. and A. Gray) Torr. Recorded flying late January through mid-May.

Etymology. The specific epithet is derived from the Latin *sex* (Brown 1956: 700), which means six, and the Latin *fasciata* (Brown 1956: 134), which means band or stripe. It references the three pairs of vittae on the scutum, a character unique within the genus *Sphecomyia*.

***Sphecomyia tsherepanovi* (Violovitsh, 1974), stat. rev. et comb. n.**
Figs 2L, 10D, 12D, 13B, 14C, 24

Criorrhina tsherepanovi Violovitsh 1974:127. Type locality. Russia: Kuril Islands, Island Sikotan. [ZISP]
Criorhina tsherepanovi Violovitsh 1976:341 – 1982: 211, 1983: 137; Peck 1988:207
Criorrhina aino Mutin and Barkalov 1990:118, not Stackelberg 1955. Misidentification
Criorhina aino of authors, not Stackelberg 1955 – Mutin and Barkalov 1997: 217; Ohishi et al. 2004: 27; Mutin 2016: 17. Misidentification.

Diagnosis. Species similar to *S. aino* or *S. pseudosphecomima* but can be distinguished by the following characters: cell c bare on basal two-thirds; ocellar triangle black pilose; silver-white pruinose; basiphallus as in Fig. 2L.

Redescription. Male. Body length: 10.9–14.2 mm. Wing length: 8.4–9.0 mm. ***Head.*** Face silver-white pruinose with shiny, black, medial vitta extending from oral margin to base of antenna; frons broad, about as long as broad at antenna, two-thirds as broad at vertex as at antenna, bare, with silver-white pruinosity along posterior rim; vertex triangular, longer than broad, shiny, with ocellar triangle entirely, or at least mostly, black pilose; postocular border silver-white pruinose; postocular pile black; occipital pile pale; male narrowly dichoptic; antenna black, mostly black pilose, with length of segments roughly in a 3:3:2 ratio.

Thorax. Sub-shiny black; postpronotum pale pilose; scutum pale pilose, except with black pile posteromedially; scutellum, postalar callus, proepimeron, posterior anepisternum pale pilose; posterior katepisternum pale pilose with broadly separated patches; anterior anepimeron pale pilose; metasternum pale pilose; postpronotum, anterior eighth of scutellum, broad posterior margin of anepisternum and dorso-posterior corner of katepisternum silver-white pruinose; area between postpronota weakly silver-white pruinose, except shiny medially; anepimeron shiny; scutum without pruinose vittae; ventral calypter with long pale pile.

Legs. Foreleg black, except reddish-yellow at apex of femur; fore tarsi slightly broadened; midleg yellow, except basal four-fifths of femur and last two tarsomeres black; hind leg reddish-yellow, except last two tarsomeres black; legs pale pilose, except black pilose on fore tibia, fore tarsi, extreme apex of fore femur and last two mid and hind tarsomeres; hind coxa silver-white pruinose.

Wing. Hyaline; microtrichia absent from following areas: cell bc; basal two-thirds of cell c; basal fourth of cell sc; cell r_1 from base almost to crossvein r-m; broad basal portion of cell br (before origin of M) and about basal two-fifths of narrower portion of this cell (caudad of spurious vein only); cell bm, except apex and narrow anterior and posterior margins of about apical fourth; broad anterior margin of cell cua; narrow, elongate, oval area proximal to vein A_1.

Abdomen. Tergites and sternites shiny to sub-shiny, black with silver-white pruinosity as follows: tergite 1 pruinose posteriorly; tergite 2 with thin, interrupted, medial band which curves posteriorly to reach the posterolateral corners; tergite 3 with thin, interrupted, medial band which does not curve anteriorly; tergite 4 with similar but thinner band; sternite 1 weakly pruinose; sternites 2 and 3 pruinose on anterior third and sub-shiny on remainder; sternite 4 with anteromedial pruinose spots; pile of abdomen pale.

Male genitalia. Surstylus not elongated, about as long as broad, curving upward ventrally; pile on anterolateral outer surface of surstylus; minute spines on ventral surface and apical half of interior lateral surface; basal fourth of the ventral surface of the surstylus produced into a lobe directed anteriorly, with minute pubescence on ventral and lateral inner surface; cerci rounded, with no invagination on posterior border; aedeagus as in Fig. 2L.

Female. Similar to male except normal sexual dimorphism.

Distribution. Japan: Hokkaido, Honshu. Russia: Kuril Islands (Fig. 24).

Biology. Collected visiting flowers of *Philadelphus satsumi* Siebold ex Lindl. and J. Paxton. Recorded flying early June through mid-July.

Remarks. See *S. aino*.

Sphecomyia vespiformis (Gorski, 1852)

Figs 2M, 4C, 16D, 17D, 18D, 19B, 21E, 22F, 24

Tyzenhauzia vespiformis Gorski 1852: 170. **Type locality.** Vilinius, Lithuania. [ZMHU]

Sphecomyia vespiformis, Wahlberg 1854: 155 – Zetterstedt 1855: 4646; 1859: 5075; Schiner 1857: 445, 1862: 367, 1864: 112; Bonsdorff 1861: 213; Siebke 1877: 50; Curran 1932: 8; Bańkowska 1963: 67; Stone et al. 1965: 612; Weisman 1965: 268, 1966a: 51, 1966b: 192; Violovitsh 1983: 146; Peck 1988: 213; Soszyński 1991: 92, 2004: 307; Bartsch et al. 1998: 53; Nielsen 1999: 10,91; Söderman 1999: 33; Haarto and Kerppola 2007: 488, 2014: 247; Karpa 2008: 17; Bartsch et al. 2009: 379; Speight 2014: 246; Pettersson and Fors 2014: 6; Mutin et al. 2016: 9; Żóralski et al. 2016: 127, 2017: 76.

Sphecomyia vittata of authors, not Wiedemann 1830 – Osten Sacken 1877: 341; Roder 1879: 96; Portschinsky 1887: 8; Aldrich 1905: 405; Kertész 1910: 349; Shannon 1925: 43; Stackelberg 1958: 244; Séguy 1961: 156; Cole and Schlinger 1969: 331; Peck 1988: 213. Misidentification.

Diagnosis. It can be confused with *S. vittata* but can be distinguished by the following characters: anepimeron not pruinose; anterior half of scutellum pruinose; sternite 2 completely black or with faint, interrupted, pruinose band anteriorly.

Redescription. Male. Body length: 14.8–15.9 mm. Wing length: 10.4–12.1 mm. ***Head.*** Face yellow pruinose with shiny, black, medial vitta extending from oral margin to base of antenna; frons enlarged antero-dorsally, longer than broad and as broad at vertex as at antenna, bare, with yellow pruinosity along posterior rim; vertex triangular, longer than broad, shiny, with ocellar triangle yellow pilose; postocular border yellow pruinose; postocular and occipital pile yellow; male narrowly dichoptic; antenna black, black pilose, with length of segments roughly in a 4:4:1 ratio.

Thorax. Matte black; postpronotum, scutum, scutellum, postalar callus, proepimeron, posterior anepisternum yellow pilose; posterior katepisternum yellow pilose with broadly separated patches; anterior anepimeron yellow pilose; metasternum yellow pilose; postpronotum, anterior half of scutellum, broad posterior margin of anepisternum and dorso-posterior corner of katepisternum yellow pruinose; anepimeron shiny; scutum with two pairs of pruinose vittae, anterior pair long running from anterior edge of scutum to transverse suture, posterior pair shorter and terminating before posterior edge; ventral calypter with long yellow pile.

Legs. Legs yellow to reddish-yellow. Legs yellow pilose.

Wing. Hyaline; microtrichia absent from following areas: cell bc; broad basal portion of cell br (before origin of M) and about basal two-fifths of narrower portion of this cell (caudad of spurious vein only); cell bm anteromedially; broad anterior margin of cell cua.

Abdomen. Tergites and sternites shiny to sub-shiny, black with yellow pruinose markings as follows: tergite 1 pruinose along posterior margin; tergite 2 with broad, interrupted, narrowing medial band which does not meet a narrow, uninterrupted posterior band in the posterolateral corners of tergite; tergite 3 with similar band, but thinner and more narrowly interrupted; pattern on tergite 4 same as tergite 3 except medial band very narrowly or incompletely interrupted; sternite 1 shiny; sternite 2 completely black or with faint, interrupted band anteriorly; sternite 3 and 4 with uninterrupted, or narrowly interrupted band anteriorly; sternites 6 to 8 pruinose; pile of abdomen yellow.

Male genitalia. Surstylus elongated, about two and a half times as long as broad, apex cute, with abrupt curve, directed ventrally; pile on dorsal surface of surstylus, increasing in length posteriorly; minute spines on ventral surface and apical three-fourth of lateral inner and outer surface; basal fourth of the ventral surface of the surstylus produced into a lobe directed posteroventrally, with minute pubescence on ventral and lateral inner surface; cerci rounded, with invagination on posterior border; aedeagus as in Fig. 2M.

Female. Similar to male except normal sexual dimorphism.

Biology. Often found in June or July along rivers and streams in *Betula* L./*Pinus* L. forest. Copulation has been observed on the trunk of *Populus tremula* L., *Crataegus maximowiczii* C.K.Schneid., *Hesperis matronalis* L., *Pimpinella saxifraga* L., *Rubus*

idaeus L., *Sorbus aucuparia* L., and *Spiraea salicifolia* L. Immature stages are not described but are probably associated with sap-runs or lesions in the trunk of *Populus tremula* (Speight 2014).

Distribution. Southern Norway to northern Sweden, Finland and Russian Karelia, the Baltic States, Poland, and throughout Siberia, reaching the Pacific coast (Fig. 24).

Sphecomyia vittata (Wiedemann, 1830)

Figs 1, 2N, 5C, 6B, 16F, 17F, 18F, 19A, 21D, 23

Chrysotoxum vittatum Wiedemann 1830: 87. **Type locality.** Unknown. LT male designated in Thompson 1988: 222 [NMW]

Psarus ornatus Wiedemann 1830: 91 – Macquart 1835: 491. **Type locality.** U.S.A.: Georgia [ZMHU]

Sphecomyia vittata, Macquart 1842: 75 – Gorski 1852: 170; Zetterstedt 1855: 4646; Osten Sacken 1875: 62, 1877: 342; Roder 1879: 96; Williston 1886: 257; Portschinsky 1887: 8; Smith 1890: 388; Hunter 1896: 101; Johnson 1900: 664, 1910: 349, 1914: 125, 1925: 178, 1929: 374; Chagnon 1901: 71; Aldrich 1905: 405; Jones 1907: 99; Osburn 1908: 14; Kertész 1910: 349; Metcalf 1913: 98, 1916: 111; Winn and Beaulieu 1915: 138; Banks et al. 1916: 192; Cockerell 1917: 16; Britton 1920: 188; Wehr 1924: 42; Shannon 1925: 43; Leonard 1928: 802; Curran 1932: 8; Winn and Maltais 1932: 53; Brimley 1938: 355; Stone (et al.) 1965: 613; Weisman 1965: 268, 1966a: 50, 1966b: 191; Cole and Schlinger 1969: 331; Waldbauer 1970: 45, 1983: 81; Shorter and Drew 1976: 89; Finnamore and Neary 1978: 172; Maier and Waldbauer 1979: 60; Waldbauer and LaBerge 1985: 101; Thompson 1988: 222.

Sphecomyia boscii Desmarest 1848: 730 – Evenhuis and Thompson 1990: 254. Type locality. U.S.A.: Carolinas. [MNHN]. Syn. n.

Diagnosis. It can be confused with *S. vespiformis* but can be distinguished by the following characters: anepimeron pruinose; anterior three-fourths of scutellum pruinose; sternite 2 with anterior corners and lateral margins pruinose.

Redescription. Male. Body length: 10.9–17.1 mm. Wing length: 7.9–12.1 mm. ***Head.*** Face yellow pruinose with shiny, black, medial vitta extending from oral margin to base of antenna; frons not enlarged antero-dorsally, longer than broad and as broad at vertex as at antenna, bare, with yellow pruinosity along posterior fourth; vertex triangular, longer than broad, shiny, with ocullar triangle yellow, black or mixed black and yellow pilose; postocular border yellow pruinose; postocular and occipital pile yellow; male narrowly dichoptic; antenna black, black pilose, with length of segments roughly in a 4:4:1 ratio.

Thorax. Matte black; postpronotum, scutum completely yellow pilose, except sometimes with black pile posteromedially; scutellum yellow pilose, except sometimes with black pile on non-pruinose portion; postalar callus, proepimeron, posterior an-

episternum yellow pilose; posterior katepisternum yellow pilose with broadly separated patches; anterior anepimeron yellow pilose; metasternum yellow pilose; postpronotum, anterior three-fourths of scutellum, broad posterior margin of anepisternum, dorso-posterior corner of katepisternum and yellow pruinose; anepimeron pruinose anteriorly; scutum with two pairs of tear shaped pruinose vittae, anterior pair short stopping before transverse suture, posterior pair longer but terminating before posterior edge; ventral calypter with long yellow pile.

Legs. Legs yellow to reddish-yellow. Legs yellow pilose.

Wing. Hyaline; microtrichia absent from following areas: cell bc; basal third of cell sc; broad basal portion of cell br (before origin of M) and about basal two-fifths of narrower portion of this cell (caudad of spurious vein only); cell bm except apex and narrow posterior margins of about apical half; broad anterior margin of cell cua.

Abdomen. Tergites and sternites shiny to sub-shiny, black with yellow pruinose markings as follows: tergite 1 pruinose along posterior margin; tergite 2 with broad, interrupted, truncate medial band which meets a broad, uninterrupted, posterior band in the posterolateral corners of tergite; tergite 3 with similar band, but more narrowly interrupted; pattern on tergite 4 same as tergite 3 except medial band very narrowly or incompletely interrupted; sternite 1 shiny; sternite 2 with anterior corners and lateral margins pruinose; sternite 3 mostly pruinose with posteromedial region of non-pruinosity, sternite 4 pruinose on anterior third and lateral margins; sternites 6 to 8 pruinose; pile of abdomen yellow.

Male genitalia. Surstylus elongated, about 2½ times as long as broad, apex rounded, directed ventrally; pile on dorsal surface of surstylus, increasing in length posteriorly; minute spines on ventral surface and apical three-fourth of lateral inner and outer surface; basal fourth of the ventral surface of the surstylus produced into a lobe directed posteroventrally, with minute pubescence on ventral and lateral inner surface; cerci rounded, with invagination on posterior border; aedeagus as in Fig. 2N.

Female. Similar to male except normal sexual dimorphism.

Distribution. Manitoba east to New Brunswick south to Florida west to New Mexico and Utah. Widespread east of the Great Plains (Fig. 23).

Biology. Collected on flowers of *Acer spicatum* Lam., *Alliaria petiolata* (M. Beib.) Cavara and Grande, *Corema* (D. Don) sp., *Cornus florida* L., *Crataegus marshallii* Eggl., *Sassafras albidum* (Nutt.) Nees, *Prunus gracilis* Engelm. and A. Gray, *Prunus serotina* Ehrh., *Prunus virginiana* L., *Aronia melanocarpa* (Michx.) Elliott, *Physocarpus opulifolius* (L.) Maxim., *Symplocos* Jacq. sp., *Corus* sp., *Viburnum cassinoides* L., *Viburnum lentago* L., *Viburnum prunifolium* L., and *Viburnum rafinesquianum* Schult. Also collected at *Acer* L. sap runs. Usually collected in deciduous woods, often near a stream or river, but has also been taken in sphagnum bog. One female has been collected in leaves at base of a hardwood tree.

Known hilltopper. Authors have personally observed specimens flying in a lazy-S-type pattern similar to that of wasps. Recorded flying early March through late July.

Remarks. Desmarest (1848) assigned the name *Sphecomyia boscii* to the specimens Latreille used to establish *Sphecomyia*. The name was forgotten until its rediscovery in

Evenhuis and Thompson (1990). We do not assign a neotype as it is uncertain if the series is lost. It is not listed among the MNHN types, nor did the primary author encounter it during a visit to the collection.

COI barcoding recovered two clusters of *S. vittata* with a maximum barcode divergence barcode of 2.41%. Specimens of both clusters were compared, and no morphological differences were found.

Sphecomyia weismani **Moran sp. n.**
http://zoobank.org/D935BC53-AAEF-475D-82EB-B4D136D93037
Figs 2O, 3B, 7D, 8D, 9D, 26

Type locality. U.S.A.: Arizona: Greenlee Co., Hannagan Meadows, 33.6392, –109.3263, 2743 m.

Types. *Holotype* male, pinned. Original label: "Hannagan Meadows, 9000' // Greenlee Co. ARIZ. // I.VII 1966 // R. F. Sternitzky" "CNC DIPTERA 91440". [1♂, CNC_DIPTERA91440, CNC]

Paratypes: U.S.A.: Arizona: Apache Co., Alpine, 33.8481, –109.1431, 2438 m, R.F. Sternitzky, 27.vi.1966, CNC91439 (1♀, CNC); 3.vii.1966, CNC91438 (1♂, CNC); Apache Co., McNary, 34.0719 -109.8550, 2225 m, R.F. Sternitzky, 5.vii.1966, CNC91441 (1♀, CNC); CNC91442 (1♂, USNM); Cochise Co., Parker Canyon, Huachuca Mountains, 31.4278, –110.4519, 1585 m, R.F. Sternitzky, 25.vi.1966, CNC91443 (1♀, CNC).

Diagnosis. It can be confused with *S. columbiana*, *S. cryptica* sp. n., *S. dyari*, *S. hoguei* sp. n., *S. oraria* sp. n., and *S. pattonii* but is easily distinguished by a scutellum with the anterior half pruinose.

Description. Male. Body length: 13.6–14.6 mm. Wing length: 9.7–11.0 mm. ***Head.*** Face yellow pruinose with shiny, black, medial vitta extending from oral margin to base of antenna; frons broad, about as long as broad at antenna, two-thirds as broad at vertex as at antenna, bare, with yellow pruinosity along posterior three-fourths; vertex triangular, longer than broad, shiny, with ocellar triangle yellow pilose; postocular border yellow pruinose; postocular and occipital pile yellow; male narrowly dichoptic; antenna black, yellow pilose, length of segments roughly in a 3:3:2 ratio.

Thorax. Sub-shiny black; postpronotum, scutum, scutellum, postalar callus, proepimeron, posterior anepisternum yellow pilose; posterior katepisternum yellow pilose with broadly separated patches; anterior anepimeron yellow pilose; metasternum yellow pilose; postpronotum, anterior half of scutellum, broad posterior margin of anepisternum and dorso-posterior corner of katepisternum yellow pruinose; area between postpronota yellow pruinose, except shiny medially; anepimeron shiny; scutum without pruinose vittae; ventral calypter with long yellow pile.

Legs. Foreleg black, except extreme apex of femur and anterior third of tibia reddish-yellow; fore tarsi slightly broadened; midleg reddish-yellow, except basal four-fifths of femur and last two tarsomeres black; hind leg reddish-yellow, except last two

tarsomeres black; legs yellow pilose, except fore tibia, fore tarsi, apex of fore femur black pilose; hind coxa yellow pruinose.

Wing. Hyaline; microtrichia absent from following areas: cell bc; broad basal portion of cell br (before origin of M) and about basal two-fifths of narrower portion of this cell (caudad of spurious vein only); cell bm except apex and narrow anterior and posterior margins of about apical fourth; broad anterior margin of cell cua.

Abdomen. Tergites and sternites shiny to sub-shiny black; with yellow pruinose markings as follows: tergite 1 pruinose along posterior margin; tergite 2 with broad, interrupted, truncate medial band which meets a narrow, uninterrupted posterior band in the posterolateral corners of tergite; tergite 3 with similar medial band, but more narrowly interrupted; pattern on tergite 4 same as tergite 3 except medial band very narrowly or incompletely interrupted; sternite 1 shiny; sternites 2 to 4 almost completely pruinose, with a triangular region of non-pruinosity posteromedially; sternites 6 to 8 pruinose; pile of abdomen and postabdomen yellow.

Male genitalia. Surstylus not elongated, about as long as broad, curving downward ventrally; pile on dorsal and apical fourth of lateral outer surface of surstylus; minute spines on ventral surface, with apical half of lateral inner surface also with spines; basal fourth of the ventral surface of the surstylus produced into a lobe directed anteriorly, with minute pubescence on ventral and lateral inner surface; cerci rounded, with no invagination on posterior border; aedeagus as in Fig. 2O.

Female. Similar to male except normal sexual dimorphism.

Distribution. Arizona (Fig. 26). Known from the Mogollon Rim and Madrean Sky Islands.

Biology. Recorded flying late June through early July.

Etymology. The specific epithet honors K. E. Weisman who published a series of four papers on *Sphecomyia* that summarized most of what was previously known about the genus.

Morphology

Sphecomyia stat. rev. is redefined as the monophyletic unit of species within Criorhinina that possess the following characters: a bare, medial vitta extending ventrally from the oral margin in both sexes (Fig. 4), a bare gena (Fig. 5), a bare katepimeron, a scutellum with at least anterior margin densely pruinose, an anterior ventral half of vein C before crossvein h without setae (Fig. 3B), and a narrow intersection of vein R_1 with vein C (Fig. 3B). While the combination of characters used to define *Sphecomyia* is unique, the subtribe Criorhinina is rife with homoplasy and the presence of one or more of these character states without all the others should not be taken as an indication a species belongs in *Sphecomyia*.

Like all members of the *Criorhina* group of genera, males of *Sphecomyia* are dichoptic. Holoptic males are only seen in the *Matsumyia* group of genera, although the character is homoplastic within that group. A bare medial vitta extending ventrally from

the oral margin is common within the Criorhinina, especially for the female sex. Rare, however, are species in which the character state is present in both the male and female sex. Within the Criorhinina, other than *Sphecomyia*, a bare medial facial vitta is to our knowledge present only in two *Criorhina* species as well as a handful of species which will be placed into the *Matsumyia* group in an upcoming paper. The presence of pile on the gena is homoplastic in all other genera except *Sphecomyia* where it is always absent.

Also completely absent in *Sphecomyia*, a pilose katepimeron is present in almost all true *Criorhina*. However, while uncommon and likely resulting from independent origins, the character state is present in other Criorhinina genera as well. Pruinosity of the scutellum is homoplastic throughout the Criorhinina, with characters states including non-pruinose, weakly pruinose and densely pruinose. However, the character state of an incompletely pruinose scutellum with at least the anterior margin densely pruinose is exclusive to *Sphecomyia*. Only *S. metallica* and *S. interrupta* do not follow this and have a completely pruinose scutellum.

The most reliable character to distinguish between the *Criorhina* group of genera and the *Matsumyia* group of genera is what we define as a narrow intersection of vein R_1 with vein C as opposed to a broad intersection. In the *Matsumyia* group of genera vein R_1 is broadly inserted (Fig. 3A), causing the width of the posterior half of cell r_1 to remain almost unchanged until vein R_1 abruptly merges with vein C. In the *Criorhina* group of genera, however, vein R_1 is what we call narrowly inserted (Fig. 3B, C), causing the width of the posterior half of cell r_1 to rapidly decrease such that vein R_1 runs alongside vein C as the two veins gradually merge together. A second reliable character aiding in separation of the two groups of genera is the presence or absence of setae on the anterior ventral half of vein C before crossvein h. Members of the *Matsumyia* group of genera are setose on this region (Fig. 3A). Members of the *Criorhina* group of genera are bare (Fig. 3B).

The character state of the distance between apices of veins R_1 and R_{2+3} longer than distance between apices of veins R_{2+3} and vein R_{4+5}+M_1 (Fig. 3B) is an exclusionary one as the character state in which it is shorter is nearly ubiquitous in the *Matsumyia* group (Fig. 3A) but also found in a subset of species placed in *Criorhina* (Fig. 3C). The character states of erect abdominal pile and appressed abdominal pile are homoplastic to some degree within the Criorhinina. However, erect abdominal pile is the only character state found in *Sphecomyia*.

Morphologically, we recognize three major lineages of *Sphecomyia*. The *vittata* group, composed of the species with pruinose vittae on the scutum, i.e., *S. brevicornis*, *S. interrupta* sp. n., *S. sexfasciata* Moran sp. n., *S. vespiforme*, and *S. vittata*. Secondly, the *pattonii* group comprised of species with broadened fore tarsi (Fig. 6A) and without pruinose vittae on the scutum, i.e., *S. aino* (Stackelberg, 1955), *S. cryptica* Moran sp. n., S. dyari, *S. hoguei* Moran sp. n., *S. oraria* Moran sp. n., *S. pattonii*, *S. pseudosphecomima* Moran sp. n., *S. tsherepanovi* (Violovitsh, 1973), and *S. weismani* Moran sp. n. The third group comprises only one species, *Sphecomyia metallica*, which has a completely pruinose scutum. *S. metallica* shares several characters with the *vittata*

group. It has elongated surstyli, with a rounded baso-ventral lobe, reminiscent of the *vittata* group and it lacks the broadened fore tarsi of the *pattonii* group.

A useful character state is pruinosity on sternites 2 to 4 (Fig. 21). Pruinosity patterns on these segments are diagnostic to a species level or almost so. Pattern A (Fig. 21A) is seen in *S. cryptica* and *S. weismani*. Pattern B (Fig. 21B) is seen in *S. dyari* and *S. hoguei*. Pattern C (Fig. 21C) is seen in *S. columbiana*, *S. oraria*, and *S. pattonii*. Pattern D (Fig. 21D) is only in *S. vittata*. Pattern E (Fig. 21E) is only found in *S. vespiformis*. Pattern F (Fig. 21F) is seen in *S. interrupta* and *S. sexfasciata*. *Sphecomyia brevicornis* proves to be somewhat of an exception. Northern specimens (i.e. Washington, British Columbia, Idaho, Montana) possess pattern G (Fig. 21G), while Californian specimens possess pattern H (Fig. 21H). In Oregon there is mixture and apparent intermediates of the two states.

Of the two genitalic characters that Weisman (1965) used to distinguish his *vittata* group, i.e. our *Sphecomyia* stat. rev., the first, a banana-shaped phallapodeme (Fig. 2), is, based upon our preliminary investigation, tenatively a synapomorphy shared with *Criorhina* s. str. The second character, a dorsal horn on the basiphallus, is homoplastic throughout Criorhinina.

While Weisman illustrated the aedeagus for each species, our investigation revealed the anterior end of the phallapodeme can vary. Some of this variation is explainable by the length of time genitalia underwent lactic acid clearing as parts of this structure readily lose coloration. Still, there seems to be natural variation in the shape of the phallapodeme such that in the absence of other characters we caution against its use diagnostically or as justification for the erection of new species. The basiphallus and distiphallus, however, do not appear to vary within species.

COI Gene Tree

DNA barcode data (5' end of the COI) were collected for all 16 morphospecies to test proposed morphological species concepts and to provide a sequence database to assist with identifications of all life stages. Complete barcodes were obtained for all species except *S. cryptica*, *S. oraria*, and *S. pseudosphecomima*. Only fragment C was obtained for *S. cryptica* and *S. pseudosphecomima*, while fragments B and C were obtained for *S. oraria*.

Three major, monophyletic lineages of *Sphecomyia* are resolved in the NJ analysis (Fig. 27) supporting the three morphological groupings. The two species for which only fragment C was obtained, *S. cryptica* and *S. pseudosphecomima*, do not resolve as discrete species in the NJ tree. The two species are lumped with *S. hoguei* and *S. columbiana* respectively. Morphology, however, indicates that this placement is likely an artifact of the short barcode length. *Sphecomyia pseudosphecomima* differs dramatically from *S. columbiana* in that it is silver pruinose on the abdomen and possesses only a single interrupted pruinose band on tergites 2 to 4. *Sphecomyia columbiana*, however,

is yellow pruinose and possesses two pruinose bands on tergites 2 to 4. For *S. cryptica*, male genitalia as well as pruinosity patterns on sternites 2 to 4 are distinct from *S. hoguei*. The future addition of A and B fragments for these species should enable their clear differentiation through barcodes.

Barcodes revealed that specimens previously identified as *Sphecomyia aino* resolved into two groupings, one from continental East Palaearctic and a second group from the Japanese and Kuril Islands. Continental *S. aino* are silver-yellow pruinose with entirely, or at least mostly, pale pile on their antennal segments and ocellar triangle. The island-dwelling *S. tsherepanovi* are silver-white pruinose with entirely, or at least mostly, black pile on their antennal segments and ocellar triangle. Additionally, the two populations were found to possess differently shaped dorsal horn on their basiphallus (Fig. 2A L). We argue that these character differences, along with the 3% difference in the DNA barcode between the two taxa, especially considering that the mainland population has little to no variation in COI even across distances greater than 3000 km, are significant enough to warrant separation into two distinct species.

For species for which multiple barcodes were obtained, only one, *S. vittata*, showed high intraspecific variation. Two clusters of *S. vittata* were recovered, resulting in a maximum barcode divergence of 2.41% within the species. Specimens of both clusters were compared, and no morphological differences were found. Two barcodes for *S. brevicornis* were recovered. One from an Alberta specimen and one from a California specimen. The two were 1.3% different, however, neither barcode was complete with the Albertan one missing data at both ends of the sequence and the Californian one missing the middle B fragment. Additional and complete sequences of both the northern and southern morphotypes of *S. brevicornis* are needed to determine whether a gradient exists or whether two discrete clusters are resolved.

Finally, unraveling the relationship of the enigmatic *S. metallica*, the only hairy-bee mimic *Sphecomyia*, with regard to the rest of the genus requires further investigation. The analysis of COI alone placed the species as sister to *Sphecomyia* as a whole. While *S. metallica* shares several characters with the *vittata* group, it is possible these are plesiomorphic and represent shared ancestral traits. Upcoming projects with a multigene phylogeny and target-enrichment data will help with this regard.

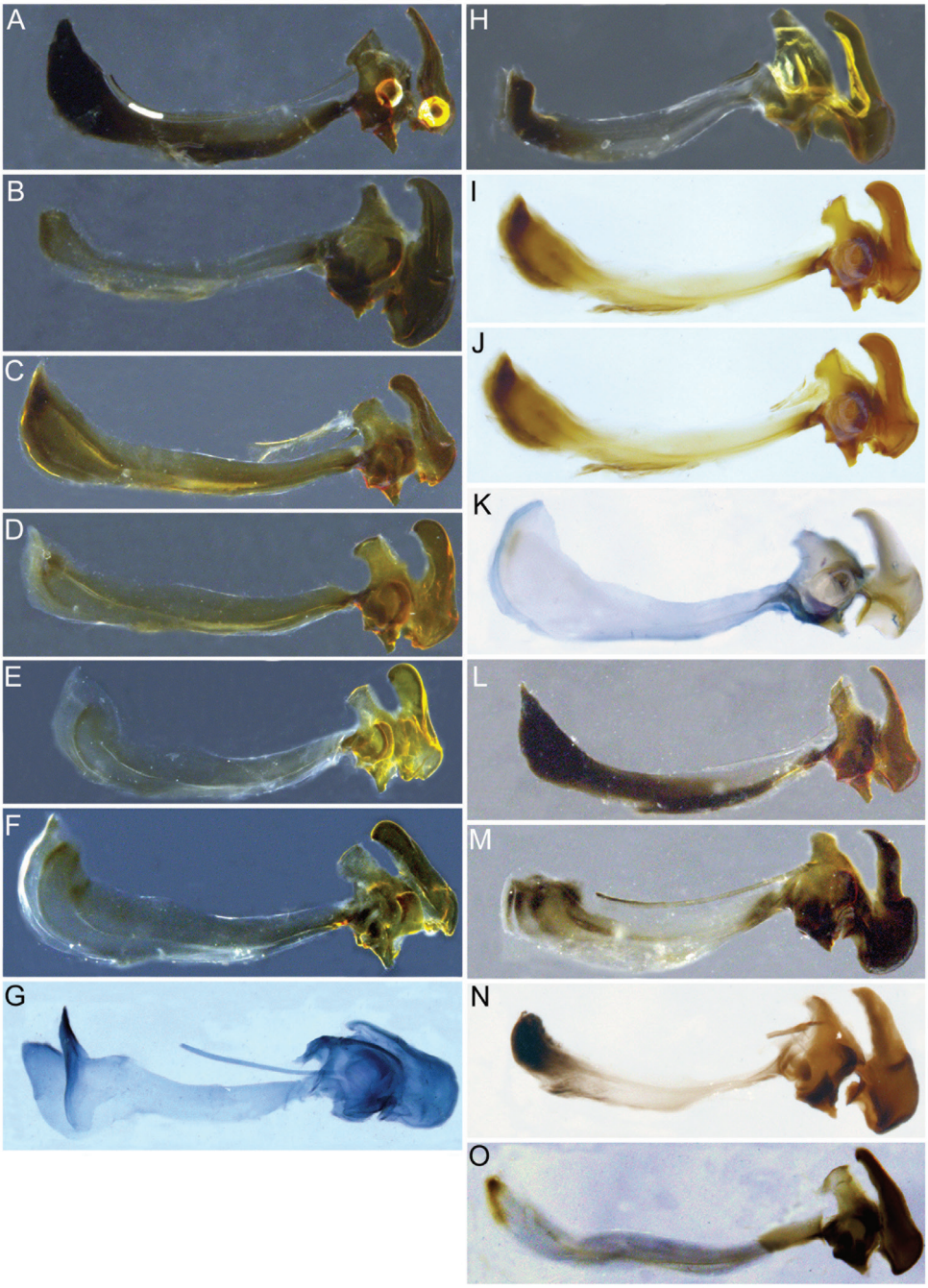

Figure 2. Aedaegal structure of *Sphecomyia*. **A** *Sphecomyia aino* **B** *Sphecomyia brevicornis* **C** *Sphecomyia columbiana* **D** *Sphecomyia cryptica* **E** *Sphecomyia dyari* **F** *Sphecomyia hougei* **G** *Sphecomyia interrupta* **H** *Sphecomyia metallica* **I** *Sphecomyia oraria* **J** *Sphecomyia pattonii* **K** *Sphecomyia sexmaculata* **L** *Sphecomyia tsherepanovi* **M** *Sphecomyia vespiformis* **N** *Sphecomyia vittata* **O** *Sphecomyia weismani.*

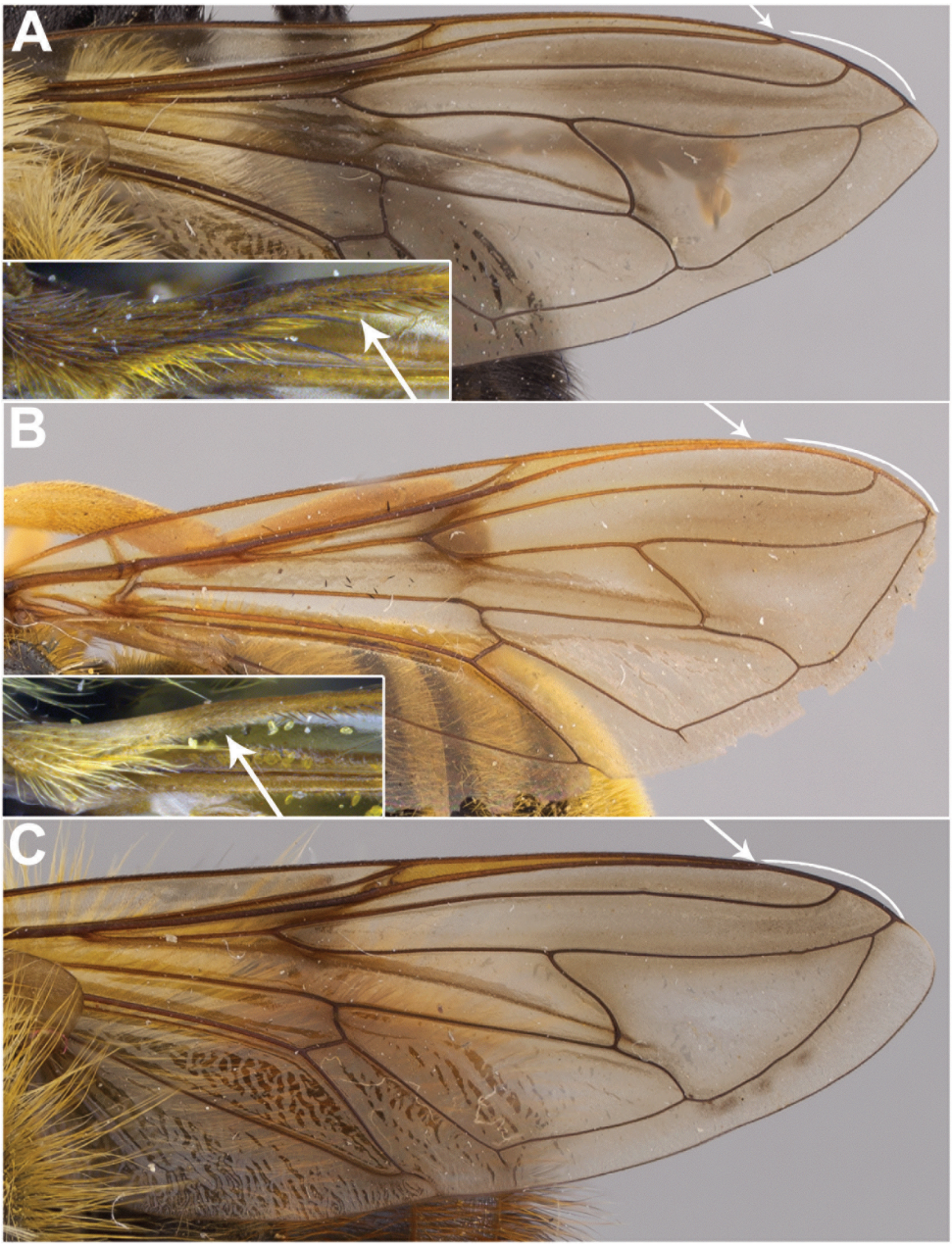

Figure 3. Intersection of vein R_1 with vein C, distance between apices of veins R_1 and R_{2+3} and apices of veins R_{2+3} and R_{4+5}+M_1 and setosity of anterior ventral half of vein C before crossvein h. **A** *Matsumyia* sp. **B** *Sphecomyia weismani* **C** *Criorhina bubulcus* (Walker, 1849).

Figure 4. *Sphecomyia* ♂ frontal habitus. **A** *Sphecomyia interrupta* **B** *Sphecomyia metallica* **C** *Sphecomyia vespiformis.*

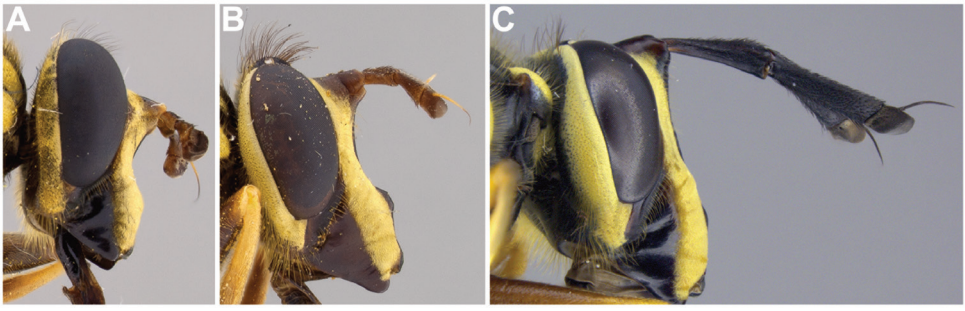

Figure 5. *Sphecomyia* ♂ antenna. **A** *Sphecomyia interrupta* **B** *Sphecomyia brevicornis* **C** *Sphecomyia vittata*

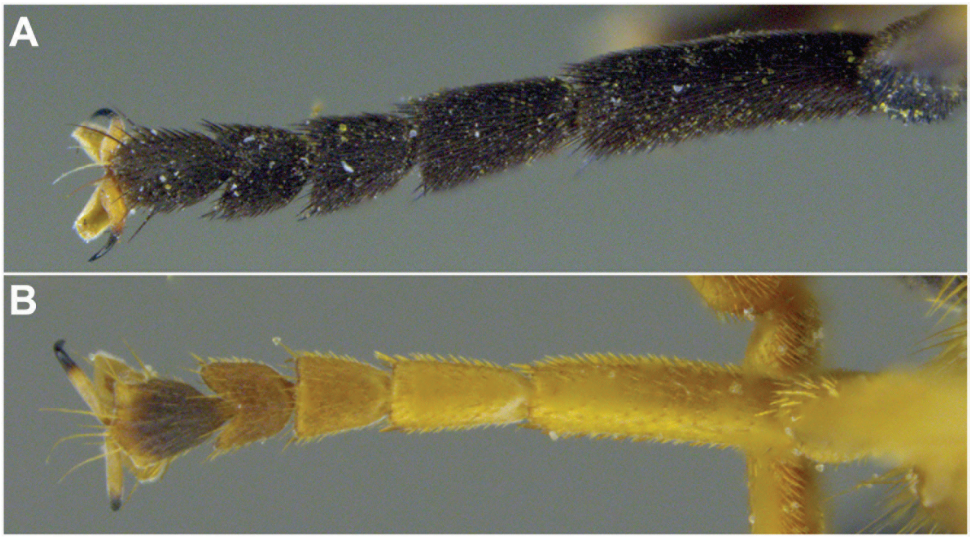

Figure 6. *Sphecomyia* fore tarsi. **A** Slightly Broadened – *Sphecomyia oraria* **B** Not Broadened – *Sphecomyia vittata*.

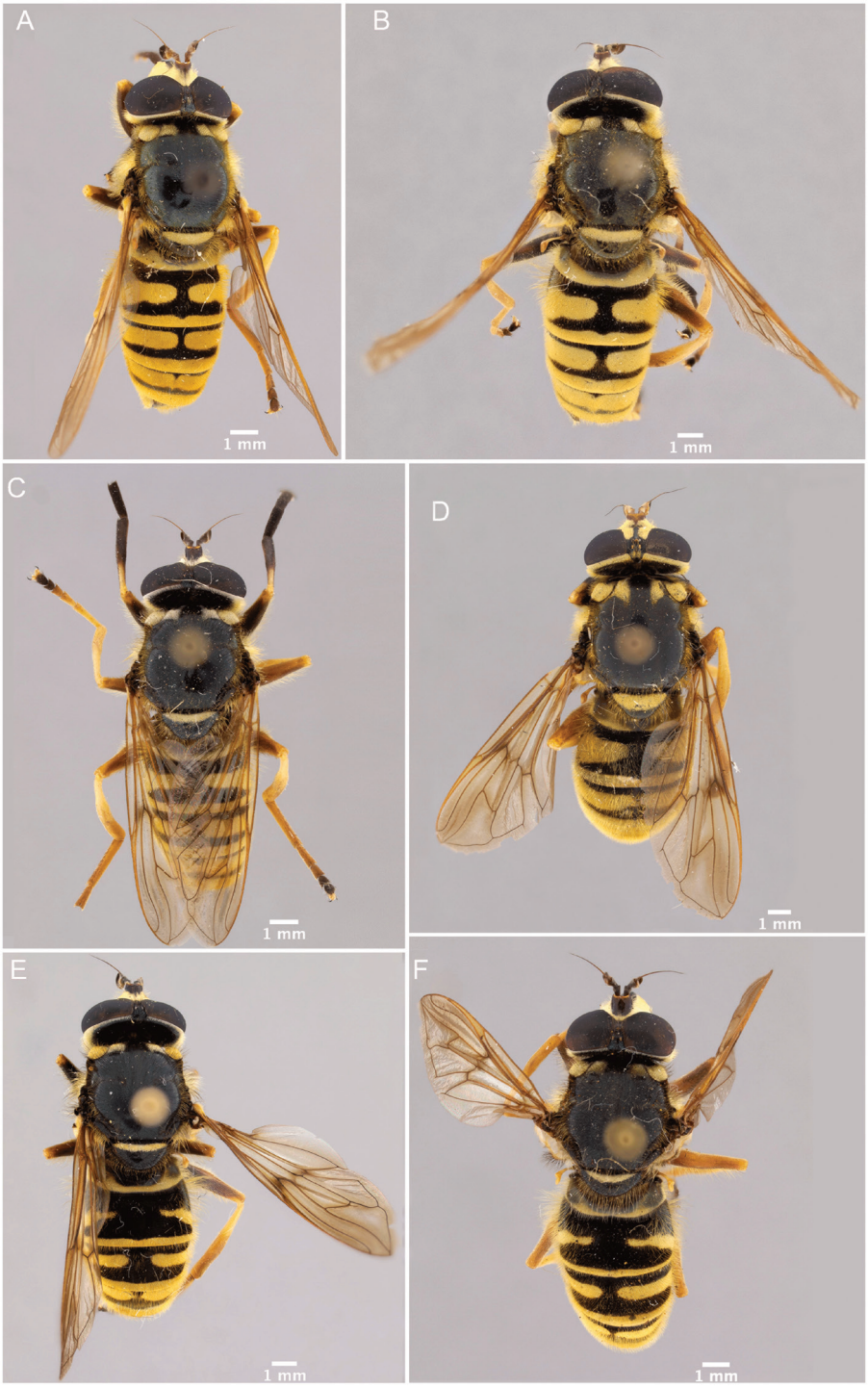

Figure 7. *Sphecomyia pattonii* group dorsal habitus. **A** *Sphecomyia dyari* **B** *Sphecomyia hoguei* **C** *Sphecomyia cryptica* **D** *Sphecomyia weismani* **E** *Sphecomyia oraria* **F** *Sphecomyia pattonii*.

Figure 8. *Sphecomyia pattonii* group lateral habitus. **A** *Sphecomyia dyari* **B** *Sphecomyia hoguei* **C** *Sphecomyia cryptica* **D** *Sphecomyia weismani* **E** *Sphecomyia oraria* **F** *Sphecomyia pattonii*.

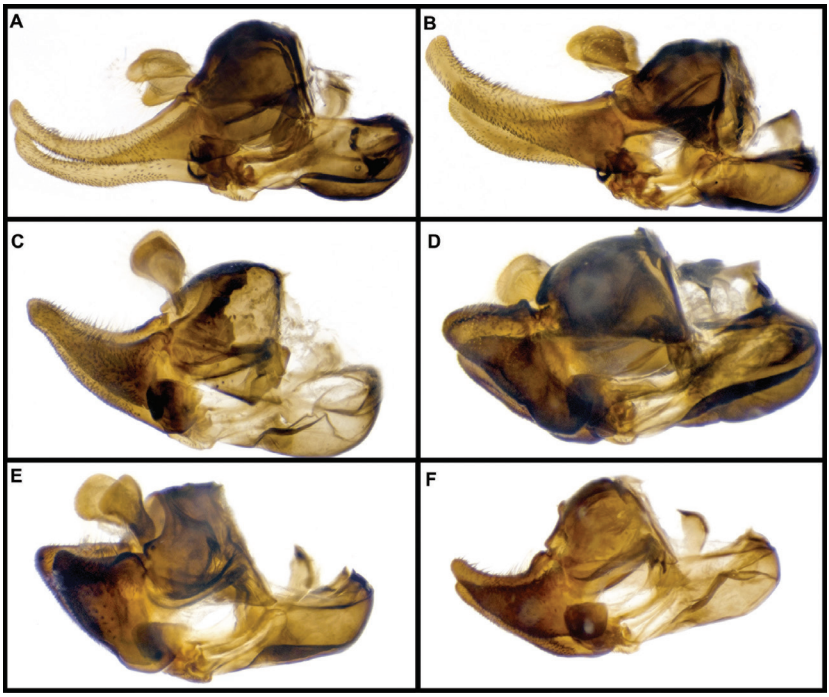

Figure 9. *Sphecomyia pattonii* group male genitalia, lateral view. **A** *Sphecomyia dyari* **B** *Sphecomyia hoguei* **C** *Sphecomyia cryptica* **D** *Sphecomyia weismani* **E** *Sphecomyia oraria* **F** *Sphecomyia pattonii.*

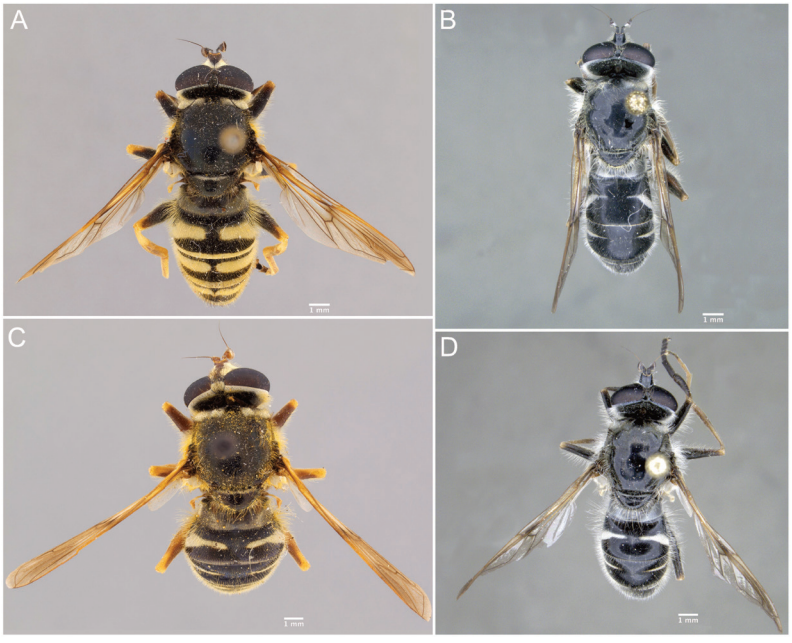

Figure 10. *Sphecomyia pattonii* group (cont.) dorsal habitus. **A** *Sphecomyia columbiana* **B** *Sphecomyia aino* **C** *Sphecomyia pseudosphecomima* **D** *Sphecomyia tsherepanovi*

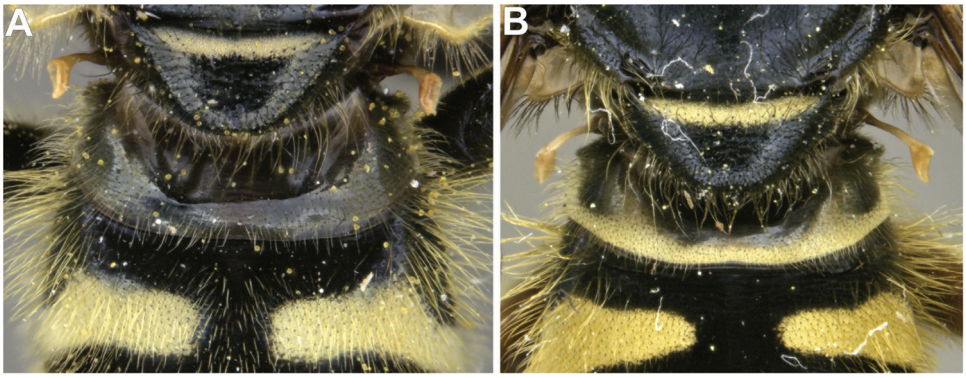

Figure 11. *Sphecomyia* tergite 1. **A** *Sphecomyia columbiana* **B** *Sphecomyia pattonii.*

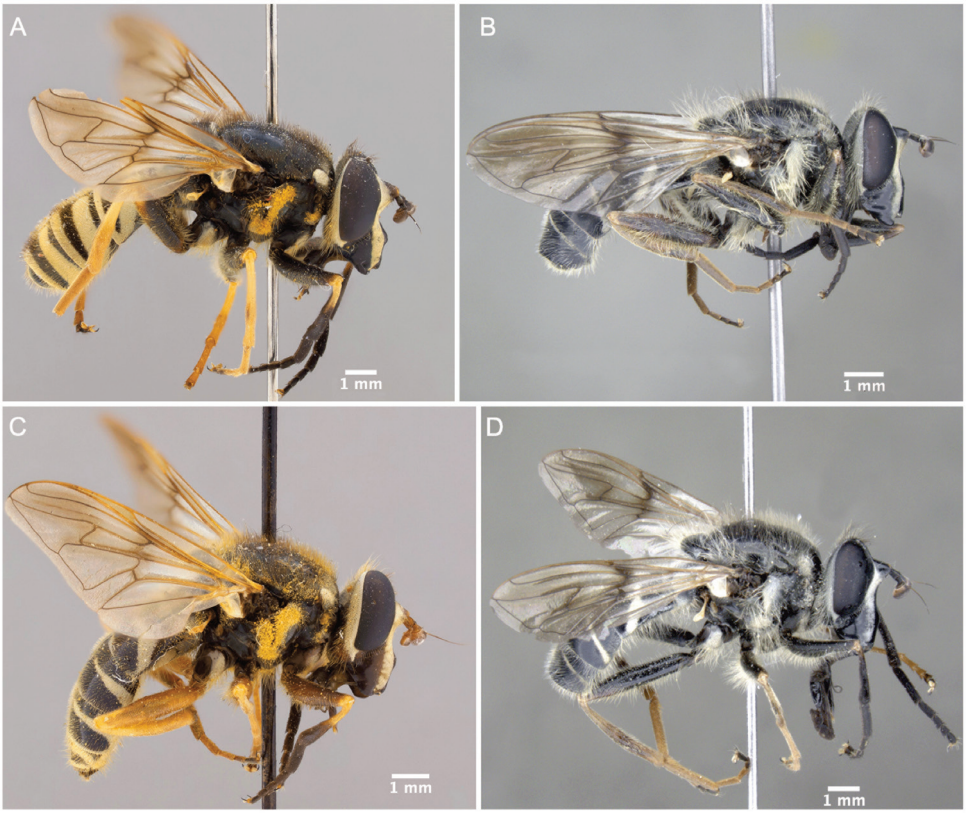

Figure 12. *Sphecomyia pattonii* group (cont.) lateral habitus. **A** *Sphecomyia columbiana* **B** *Sphecomyia aino* **C** *Sphecomyia pseudosphecomima* **D** *Sphecomyia tsherepanovi*.

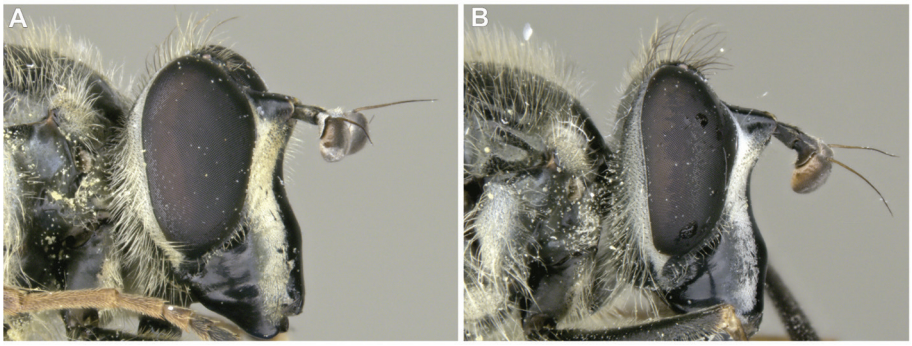

Figure 13. *Sphecomyia pattonii* group (cont.) head in lateral view. **A** *Sphecomyia aino* **B** *Sphecomyia tsherepanovi*.

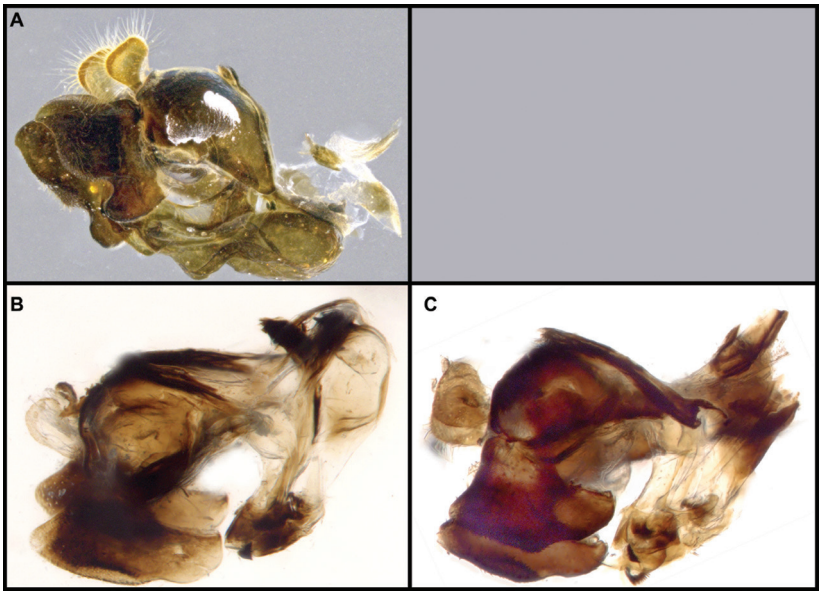

Figure 14. *Sphecomyia pattonii* group (cont.) male genitalia. **A** *Sphecomyia columbiana* **B** *Sphecomyia aino* **C** *Sphecomyia tsherepanovi*.

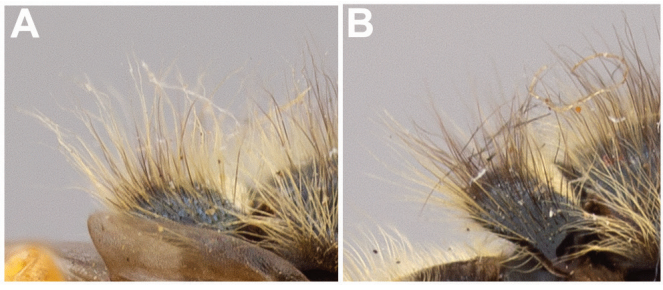

Figure 15. Scutellum pile. **A** *Sphecomyia cryptica* **B** *Sphecomyia oraria*.

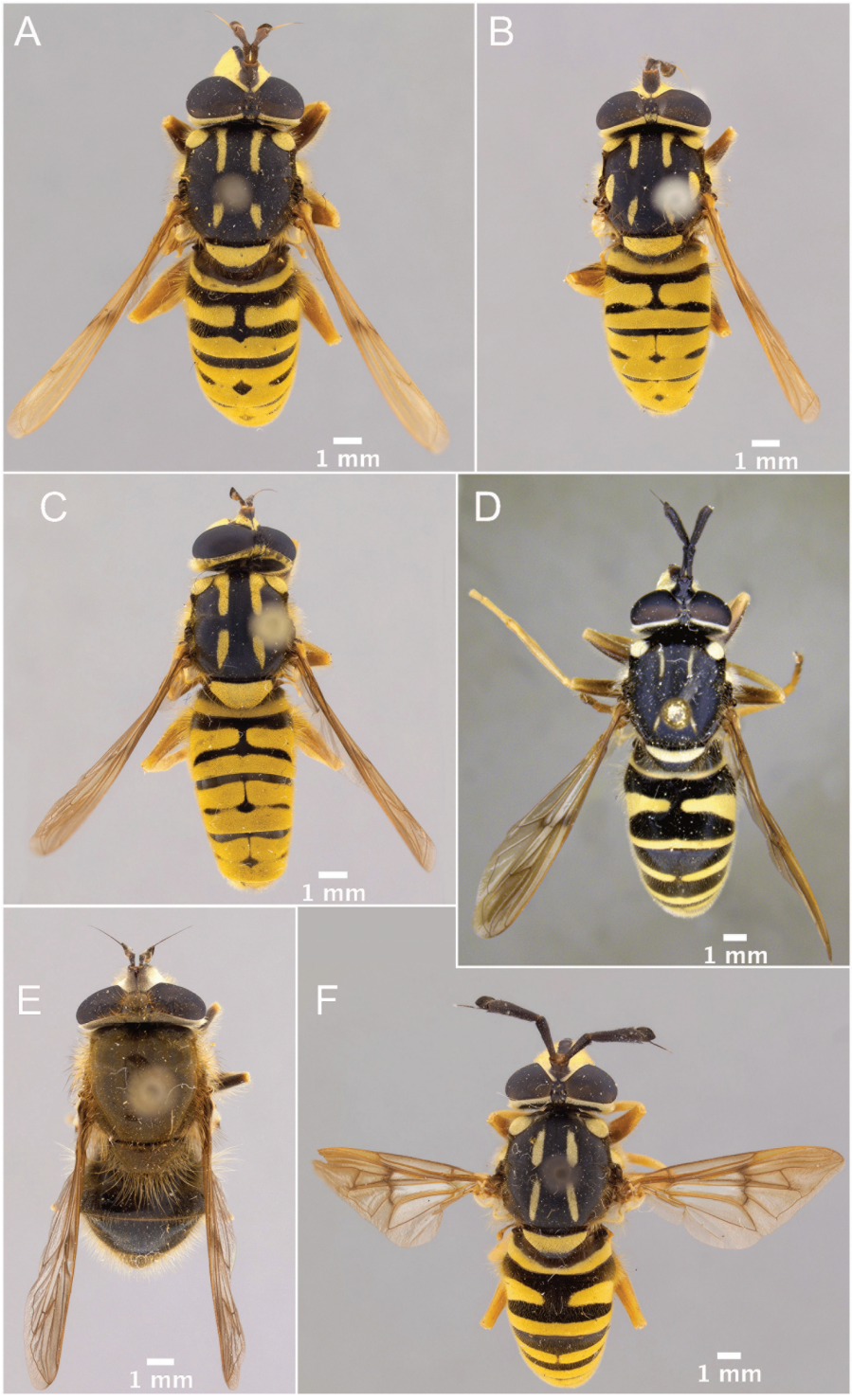

Figure 16. *Sphecomyia vittata* group dorsal habitus. **A** *Sphecomyia brevicornis* **B** *Sphecomyia sexfasciata* **C** *Sphecomyia interrupta* **D** *Sphecomyia vespiformis* **E** *Sphecomyia metallica* **F** *Sphecomyia vittata,*

Figure 17. *Sphecomyia vittata* group lateral habitus. **A** *Sphecomyia brevicornis* **B** *Sphecomyia sexfasciata* **C** *Sphecomyia interrupta* **D** *Sphecomyia vespiformis* **E** *Sphecomyia metallica* **F** *Sphecomyia vittata*

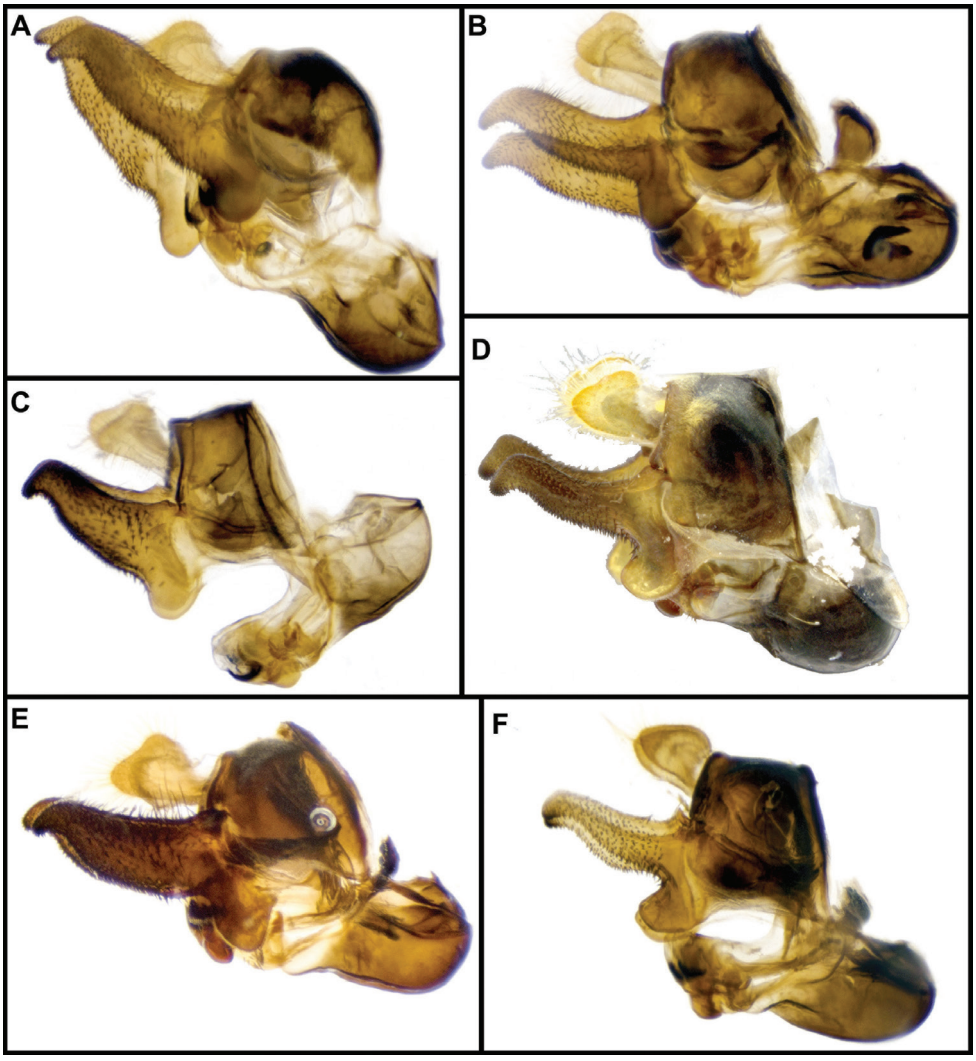

Figure 18. *Sphecomyia vittata* group male genitalia. **A** *Sphecomyia brevicornis* **B** *Sphecomyia sexfasciata* **C** *Sphecomyia interrupta* **D** *Sphecomyia vespiformis* **E** *Sphecomyia metallica* **F** *Sphecomyia vittata*.

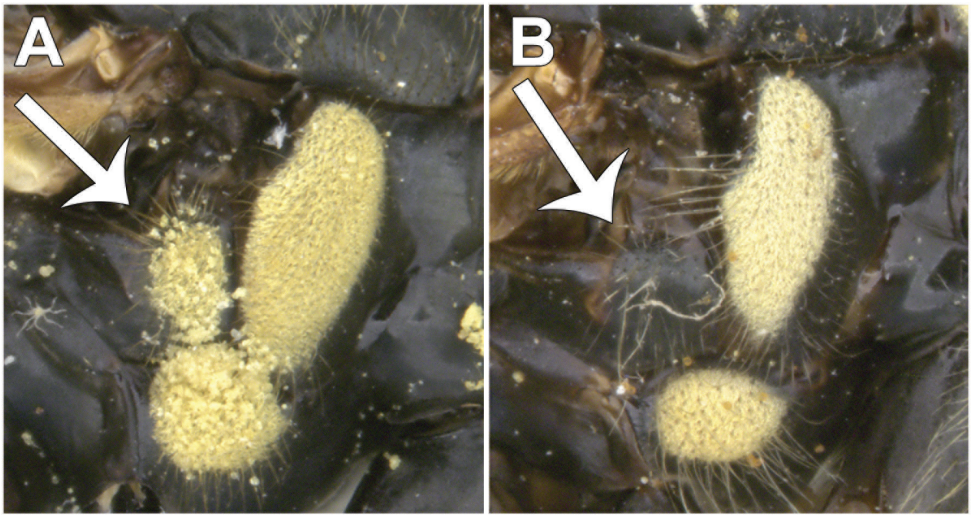

Figure 19. Anepimeron, lateral view. **A** *Sphecomyia vittata* **B** *Sphecomyia vespiformis.*

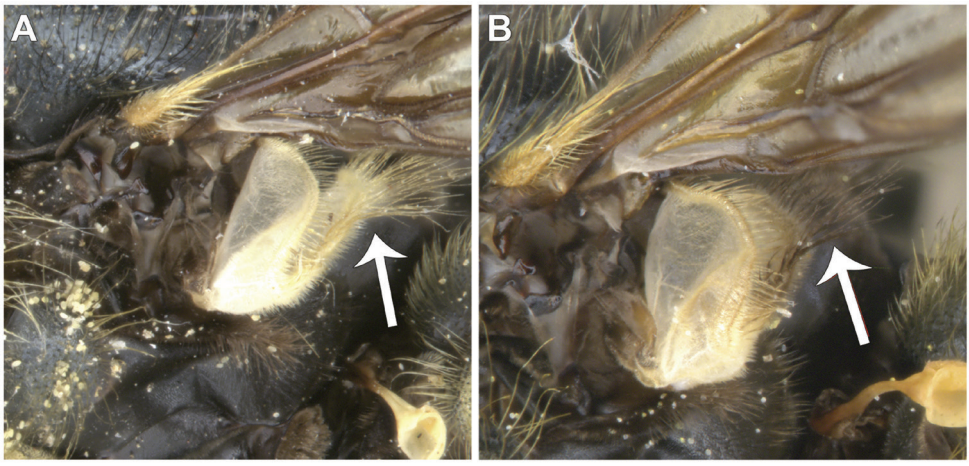

Figure 20. Calypter, lateral view. **A** *Sphecomyia oraria* **B** *Sphecomyia pattonii.*

Figure 21. *Sternite pruinosity.* **A** *Sphecomyia cryptica* **B** *Sphecomyia dyari* **C** *Sphecomyia oraria* **D** *Sphecomyia vittata* **E** *Sphecomyia vespiformis* **F** *Sphecomyia interrupta* **G** *Sphecomyia brevicornis* **H** *Sphecomyia brevicornis.*

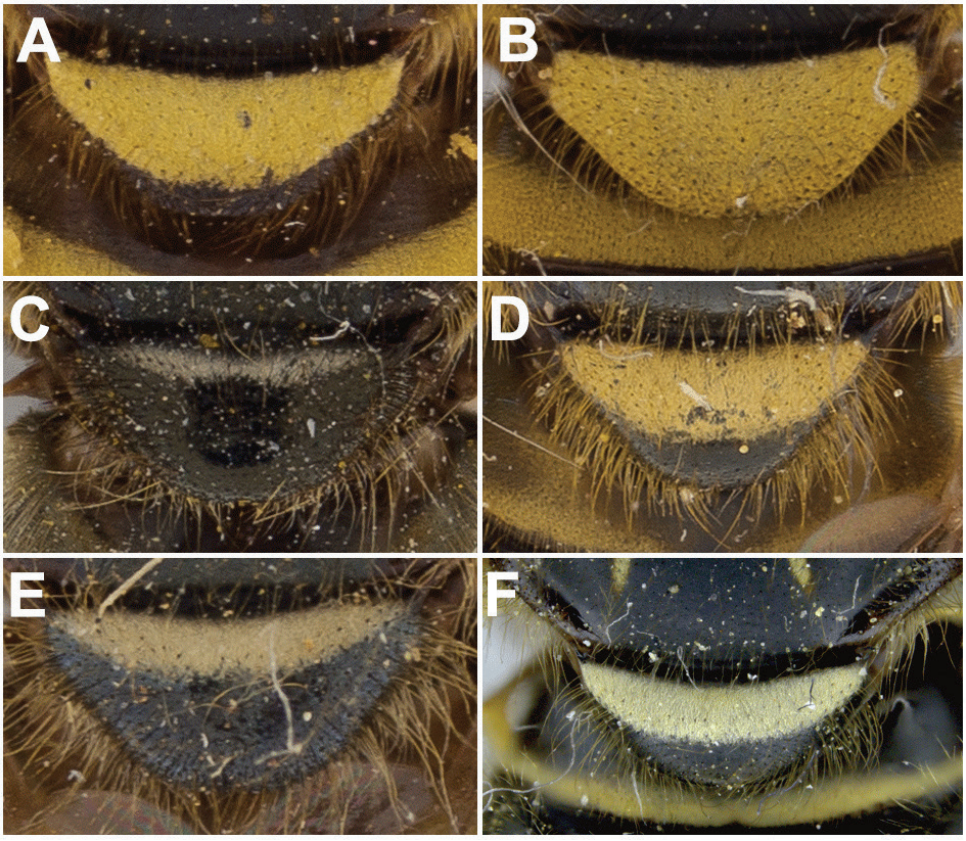

Figure 22. Scutellum pruinosity. **A** *Sphecomyia brevicornis* **B** *Sphecomyia interrupta* **C** *Sphecomyia columbiana* **D** *Sphecomyia weismani* **E** *Sphecomyia cryptica* **F** *Sphecomyia vespiformis*

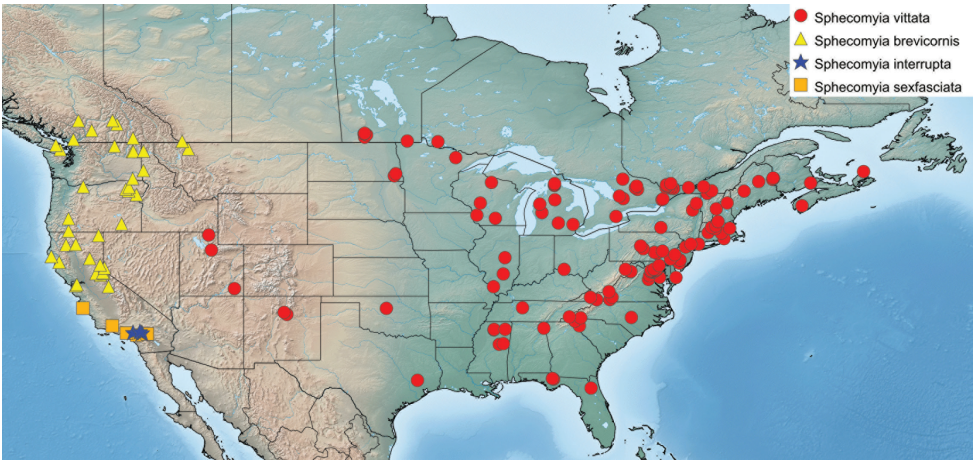

Figure 23. *Sphecomyia vittata* group distribution.

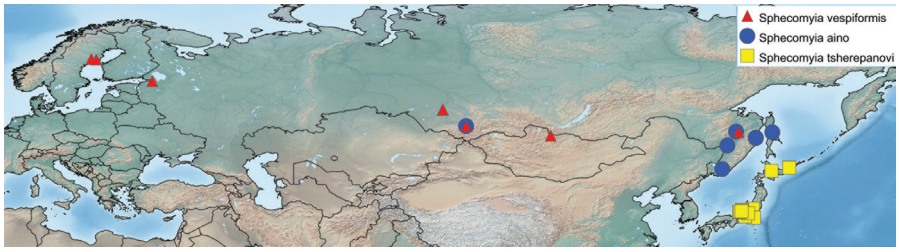

Figure 24. Old World *Sphecomyia* distribution.

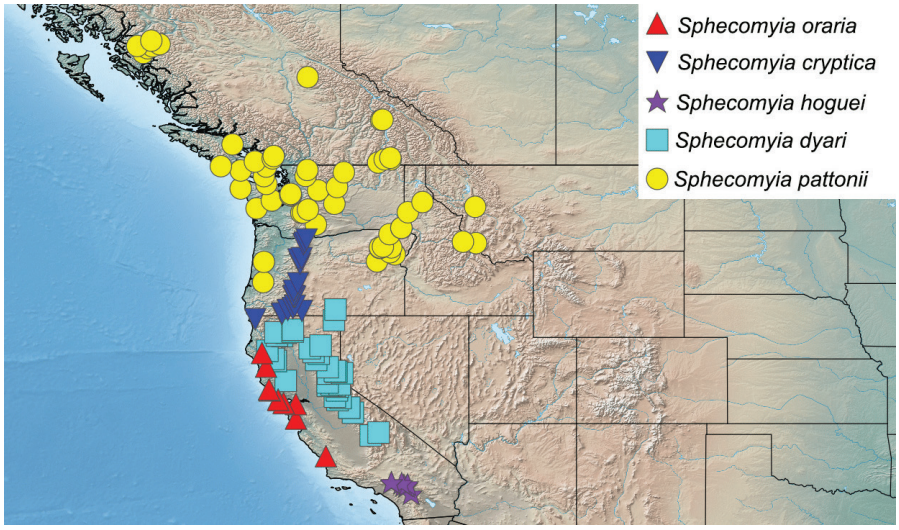

Figure 25. *Sphecomyia pattonii* group distribution.

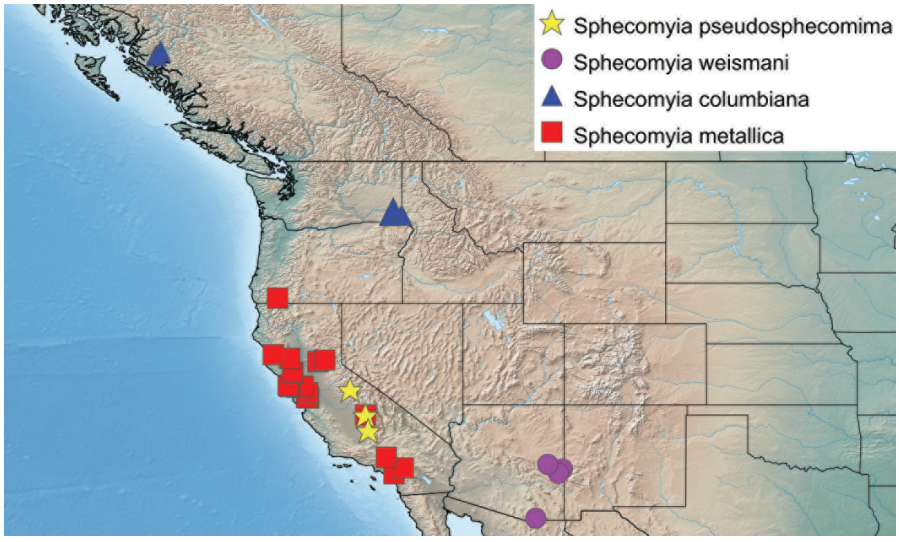

Figure 26. *Sphecomyia pattonii* group (cont.) and *Sphecomyia metallica* distribution.

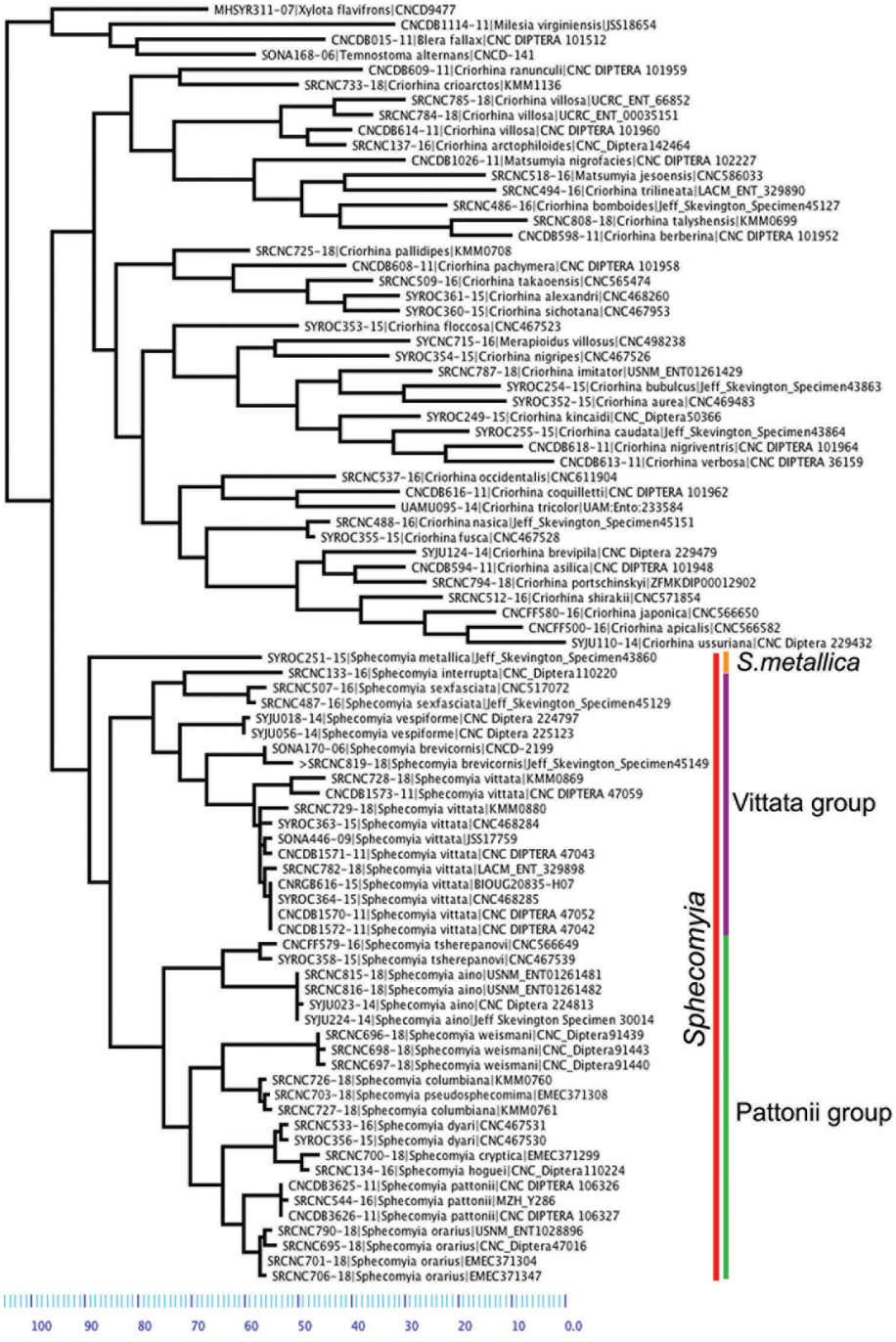

Figure 27. Neighbor Joining Tree.

Conclusions

We redefine *Sphecomyia* stat. rev. as the monophyletic unit of Criorhinina containing all species possessing a bare, medial vitta extending ventrally from the oral margin in both sexes, a bare gena, a bare katepimeron, an anterior ventral half of vein C before crossvein h without setae, and a narrow intersection of vein R_1 with vein C. This redefinition requires the transfer of *Criorhina metallica*, *Criorhina aino*, and *Criorhina tsherepanovi* to *Sphecomyia*, as they fulfill these requirements, and these new combinations are supported by the COI gene tree. Conversely, removal of three species from *Sphecomyia* and their placement in *Criorhina* is supported by the molecular data and by morphological evidence in their possession of completely pruinose face in the male, a non-pruinose scutellum, appressed pile on the abdomen and a keeled, laterally sclerotized phallapodeme. The species are *Criorhina fusca* (Weisman), comb. n., *C. nasica* (Osburn), comb. n., and *C. occidentalis* (Osburn), comb. n.

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Supplementary material 1

***Sphecomyia* specimen data**

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The sea cucumber *Holothuria lineata* Ludwig, 1875 (Holothuroidea, Aspidochirotida, Holothuriidae) re-described from the newly found type

Yves Samyn[1], Claude Massin[2], Didier Vandenspiegel[2]

1 *Royal Belgian Institute of Natural Sciences, Vautierstraat 29, B-1000 Brussels, Belgium* **2** *Royal Museum for Central Africa, Leuvensesteenweg 13, B-3080 Tervuren, Belgium*

Corresponding author: *Yves Samyn* (ysamyn@naturalsciences.be)

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Abstract

A re-description of the little-known holothurian species *Holothuria* (*Lessonothuria*) *lineata* Ludwig, 1875 is given. It is based on the single recovered type specimen and an individual recently collected on Glorioso Islands, near Madagascar. A key to separate three closely related and commonly confused species, i.e., *Holothuria* (*Lessonothuria*) *pardalis* Selenka, 1867, *Holothuria* (*Lessenothuria*) *verrucosa* Selenka, 1867 and *Holothuria* (*Lessonothuria*) *insignis* Ludwig, 1875, is presented.

Keywords

Biodiversity, synonymy, taxonomy

Introduction

Currently approximately 150 species are recognised within the genus *Holothuria* Linnaeus, 1767 (Samyn et al. 2005). However, this is a considerable underestimation of the real number of species in this mega-diverse genus in which up to 200 species have been estimated (Honey and Solis-Marin 2018). Unfortunately, many of the recognised species are so poorly described that identification of new material remains problematic. *Holothuria* (*Lessonothuria*) *lineata* Ludwig, 1875 is such a case. Even though this spe-

cies has been cited more than 30 times in the literature, an illustration of the ossicle assemblage is present only in the original description (Ludwig 1875). A colour picture of the external appearance of *H.* (*L.*) *lineata* is given only in a single recent publication (Mulochau and Conand 2008). Ludwig's (1875) drawings of the ossicle assemblage, albeit of a good quality, do not meet today's standard and thus require a re-description.

Study of the lectotype (designated by Rowe, in Rowe and Gates 1995: 291) and an additional voucher specimen from Glorioso Islands allowed us to define the boundaries of this species much more clearly. We consider *H.* (*L.*) *lineata* as valid species (see also Rowe 1989, Rowe and Gates 1995), contrary to Panning (1935) and Clark (1946) who considered it to be a junior subjective synonym of *Holothuria pardalis* Selenka, 1867.

Materials and methods

Ossicles were removed from various tissues (tentacles, dorsal and ventral body wall, dorsal papillae, and ventral tube feet) of the lectotype and the specimen from Glorioso Islands in household bleach and were observed with light and scanning electron microscopy (*SEM*) (Samyn et al. 2006; 2007). For light microscopy, permanent slides are deposited in the collection of the Royal Belgian Institute of Natural Sciences (RBINS) (I.G. 30872/HOL.1735/1-7). For SEM, samples were dried and mounted on aluminium stubs, coated with gold in a sputter coater, and observed with a JEOL JSM-5400LV. The specimen of *Holothuria lineata* from Glorioso Islands has been deposited in the collection of the RBINS (I.G. 30872/HOL.1735). The lectotype remained in the collection of the Zoological Museum Hamburg (ZMH E. 2585).

Taxonomy

***Holthuria* (*Lessonothuria*) *lineata* Ludwig, 1875**
Figs 1A, B; 2; 3A–J; 4A–I

Holothuria lineata Ludwig, 1875: 103, pl. 2, fig. 42a-e; Ludwig 1880: 7; Ludwig 1882: 136; Ludwig 1883: 170; Bell 1884: 152; Lampert 1885: 63, fig. 26; Théel 1886: 225; Bell 1887: 140; Fisher 1907: 664; Pearson 1910: 179; Mitsukuri 1912: 118 (cited as a junior subjective synonym of *H. pardalis*); Clark 1925: 103; Panning 1935: 3 (cited as a junior subjective synonym of *H. pardalis*); Clark 1946: 437 (cited as a junior subjective synonym of *H. pardalis*); Sastry 2005: 105 (*H. lineata*; Bell 1887 non *H. lineata* Ludwig 1875, cited as a synonym *of H. pardalis*); Sastry 2007: 222 (*H. lineata* ; Bell 1887 non *H. lineata* Ludwig 1875, cited as a synonym *of H. pardalis*).

? *Holothuria lineata;* Mulochau and Conand 2008: 36, fig. 3i.

Holothuria (*Lessonothuria*) *lineata*; Rowe 1989: 282; Marsh et al. 1993: 64; Marsh 1994: 10; Rowe and Gates 1995: 291; Marsh 2000: 26; Lane et al. 2000: 488; Samyn 2003: 39; Paulay 2003: 578; Thandar 2008: 53, fig. 20A–K.

Holothuria (*Lessonothuria*) *pardalis*; Liao and Clark, A.M., 1995: 438; Liao 1997: 105; Massin 1999: 25, figs 18a–j, 19 (non *Holothuria pardalis* Selenka, 1867).
Holothuria cf. *pardalis*; Mulochau and Conand 2008: 36, fig. 3j.
? *Labidodemas punctulatum* Haacke, 1880: 47.

Type material. Lectotype *H. lineata* ZMH E. 2585 Bowen (Queensland, Australia), collection date and depth unknown, A Dietrich leg., lectotype (University of Hamburg, Zoological Museum Hamburg); formerly MG 9942 (Museum Godeffroy, Hamburg). ***Other type material:*** 18 specimens according to Ludwig (1875); none recovered. ***Other material:*** Glorioso Islands, 26.iv.2008, 1 m depth, Th. Mulochau leg., RBINS I.G.30872/HOL.1735 (one specimen of *H. lineata*); Indonesia, S.W. Sulawesi, 5 m depth, C Massin leg., 23.ix.1994, Pulau, Barang-Lompo, RBINS I.G. 28251/HOL.104).

Type locality. Bowen (Queensland, Australia) (Ludwig, 1875).

Description of ZMH E. 2585, lectotype from Bowen, Australia. (Fig. 1A, B) Specimen well preserved, poorly relaxed, partly eviscerated (part of gut missing). Body form cylindrical with extremities moderately fusiform. Length 62 mm; anterior and posterior width 7 mm; mid-body width 14 mm. Mouth and anus terminal. Colour of dorsal and ventral body wall yellow to beige irregularly marbled with brown; narrow longitudinal line along the dorsal ambulacrae clearly visible. Body wall slightly rough to the touch, ca. 1 mm thick. Position of ventral and dorsal tube feet and/or papillae difficult to determine due to poor relaxation, but tube feet appear more numerous on ventral than on dorsal surface; distribution seemingly uniform over total surface. No papillae or other appendages observed around the anus. Number of tentacles, Polian vesicles, stone canals, and shape of the calcareous ring could not be determined without causing irreversible damage to the lectotype. No Cuvierian tubules observed.

Ossicles of tentacles (from tips only, as due to contraction of specimen, shafts were not accessible) comprise few straight or slightly curved rods, 25–110 μm long with spiny extremities, sometimes perforated (Figure 2A). Ossicles of ventral and dorsal body wall, ventral tube feet, and dorsal papillae comprise tables, buttons, and rods. Tables of ventral body wall and tube feet very low, nearly always reduced to the disc, with four reduced pillars; disc 38–55 μm across, perforated by 4–5 holes; edge of disc with large blunt spines (Figure 2B). Buttons of ventral body wall and ventral tube feet generally smooth, 30–60 μm long, with 1–5 pairs of holes (Figure 2C); holes very large or nearly fully obliterated; irregular buttons numerous, some being intermediary between buttons and rods (Figure 2D). Rods of ventral tube feet wide, slightly curved, 100–150 μm long, with perforated extremities (Figure 2E). Same type of ossicles in dorsal body wall and dorsal papillae, but tables slightly larger dorsally than ventrally, 50–63 μm across (Figure 2F); spire very low ending in a partial crown of spines, sometimes fully developed bearing eight spines; edge of disc spiny; disc perforated by four central holes and eight peripheral holes. Buttons 40–65 μm long, with 3–5 pairs of holes; surface of buttons slightly knobbed; holes very large or nearly obliterated (Figure 2G). Rods of dorsal papillae 100–200 μm long, smooth with perforated extremities (Figure 2H). Intermediate form between rods and buttons very rare (Figure 2I). No ossicles observed in longitudinal muscles, cloaca, digestive tract, and respiratory trees.

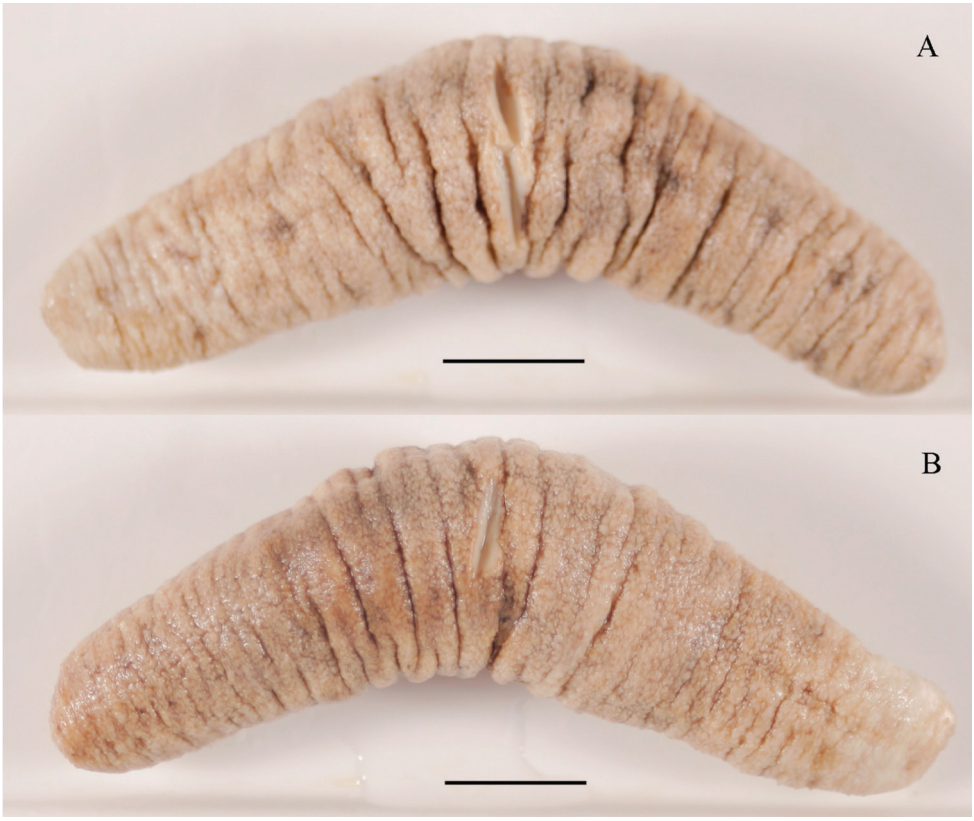

Figure 1. *Holothuria* (*Lessonothuria*) *lineata* Ludwig, 1875. **A** Dorsal view of the lectotype (ZMH E. 2585) **B** ventral view of the lectotype (ZMH E. 2585). Scale bars: 10 mm.

Description of RBINS I.G. 30872/HOL.1735, non-type material from Glorioso Islands. (Fig. 3) Single specimen well preserved, poorly relaxed. Body form cylindrical, slightly tapering at both extremities. Length 53 mm; anterior width 20 mm; posterior width 22 mm. Mouth and anus terminal. Mouth surrounded by a circle of white papillae. Colour of body wall beige-brown dorsally and beige ventrally; complete body surface speckled with minute brown dots; laterally and ventrally some transversal brown lines distinguishable; dorsal surface with conspicuous longitudinal lines along the ambulacrae and with brown blotches. Body wall soft to the touch, ca. 1.5 mm thick. Tube feet large, cylindrical, yellow with a large sucker; spread all over the ventral and dorsal surface, without alignment, more densely crowded ventrally than dorsally. Number of tentacles could not be determined without causing irreversible damage to the specimen. Calcareous ring white, extremely narrow (barely visible with the naked eye). Longitudinal muscles huge, bifid, cylindrical (3.2–5.3 mm across). Number of Polian vesicles and stone canals could not be determined. Cuvierian tubules not observed. Digestive tract full of white calcareous sand with large pieces (2 × 4 mm) of *Halimeda* sp.

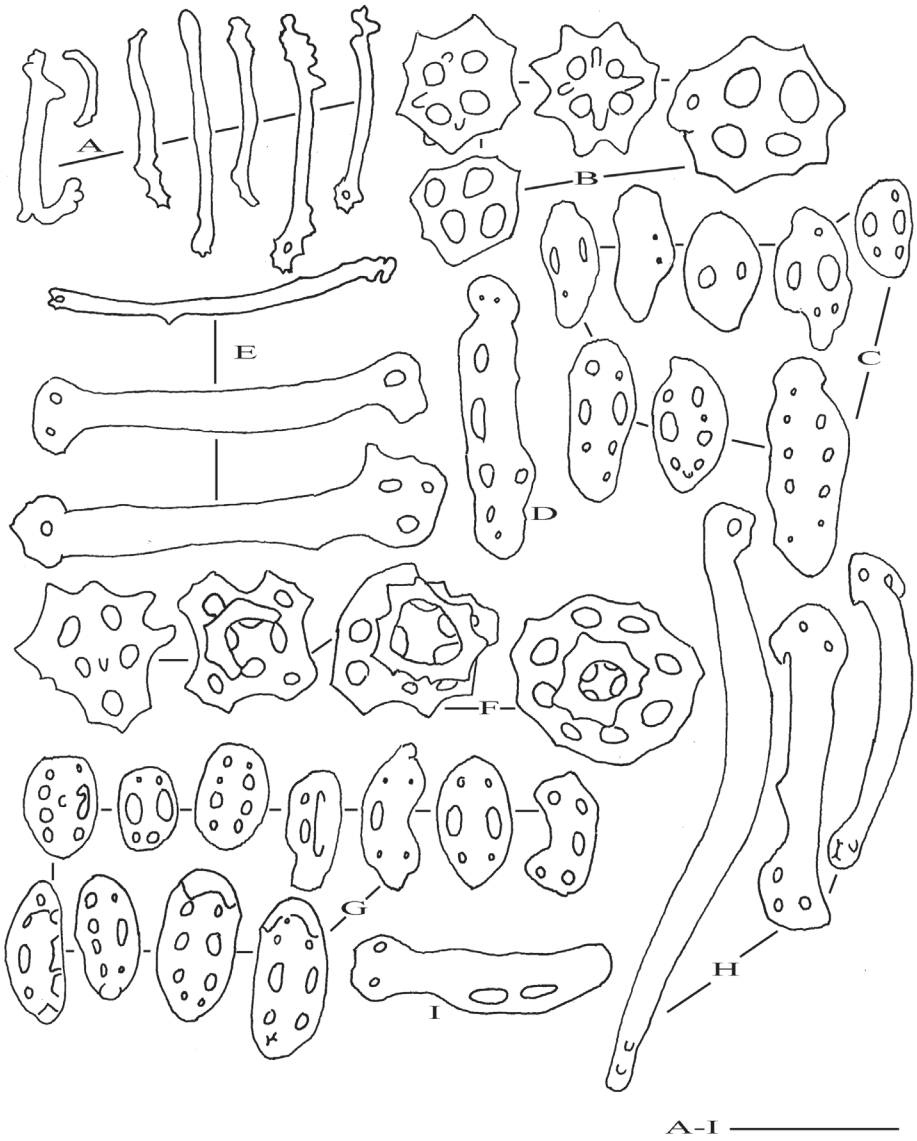

Figure 2. *Holothuria* (*Lessonothuria*) *lineata* Ludwig, 1875 (ZMH E. 2585, lectotype). **A** Rods of tentacles **B** tables of ventral body wall and ventral tube feet **C** buttons of ventral body wall and ventral tube feet **D** large button of ventral body wall **E** perforated rods of ventral tube feet **F** tables of dorsal body wall and dorsal papillae **G** buttons of dorsal body wall and dorsal papillae **H** perforated rods of dorsal papillae **I** Rod-shaped button of dorsal papillae. Scale bar: 50 μm.

Ossicles of tentacles (mainly from the shafts) comprise rods only, 150–260 μm long, smooth, perforated or slightly branched at extremities (Figure 4A). Ventral and dorsal body wall hold tables and buttons (Figure 4B, C, F, G). Ventrally, buttons 40–60 μm long, with 1–4 pairs of holes, mostly smooth; tables with spire low or completely reduced

Figure 3. *Holothuria* (*Lessonothuria*) *lineata* Ludwig, 1875. Dorsal view of the specimen collected from Glorioso Islands; photograph by T Mulochau.

to the disc, 45–55 μm across; table discs perforated by four large central holes and 0–8 small peripheral holes; rim of disc with strong spines. Dorsally, buttons more irregular than those of ventral body wall, some with only a single row of holes; tables similar to those of ventral body wall. Ventral tube feet present buttons, tables, rods, and a single-piece end-plate of 100–200 μm across (Figure 4I). Dorsal papillae devoid of perforated plates; but with numerous, slender, 110–200 μm long rods; tables in shape and size largely as in body wall, 30–50 μm across; and irregular buttons, 35–60 μm long, perforated by 1–4 pairs of holes. Ventral tube feet with the same ossicle assemblage as dorsal papillae (Figure 4E) but, slender rods scarcer, and perforated plates, 140–160 μm long, perforated by two rows of holes, present, surrounding single-pieced end-plate of 350–400 μm across; buttons 35–60 μm long, smooth or slightly knobbed; most with two rows of holes, but many irregular ones also; buttons reduced to one row of holes very rare. No ossicles observed in longitudinal muscles, cloaca, digestive tract, and respiratory trees.

Distribution. Hawaiian Ids (USA) (Fisher, 1907), Johnston Is. (USA), Mariana Ids (Guam, USA) (Paulay, 2003); Australia (NE, SE, NW, and N coasts, QLD, Thursday Is, NSW, WA, NT, Norfolk Is, Lord Howe Is., Montebello Islands, Ashmore & Cartier Islands, Tasman Sea) (Rowe 1989; Rowe and Gates 1995; Marsh 2000), Andaman Islands (Bell 1887); Sulawesi (Indonesia) (Massin 1999), Japan (Mitsukuri

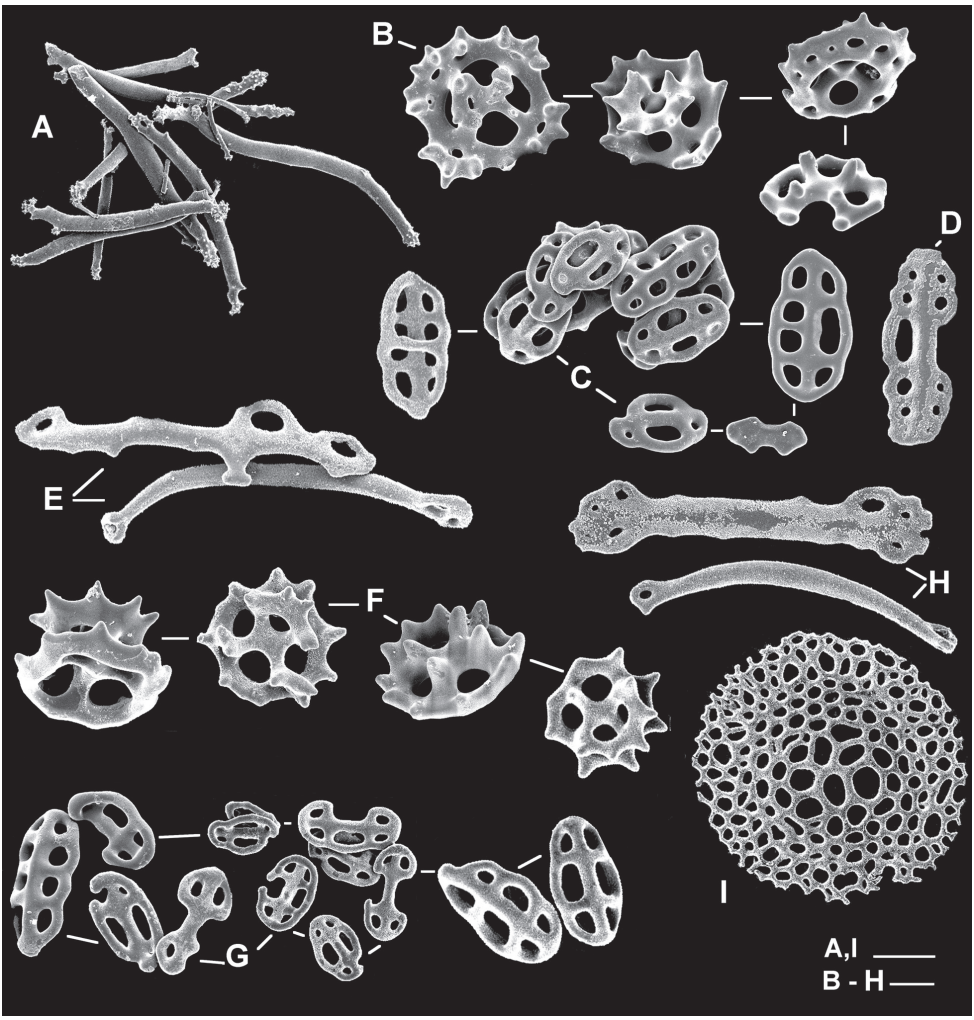

Figure 4. *Holothuria* (*Lessonothuria*) *lineata* Ludwig, 1875 (IRSNB I.G. 30872/HOL.1735). **A** Rods of tentacles **B** tables of ventral body wall and ventral tube feet **C** buttons of ventral body wall and ventral tube feet **D** rod-shaped button of ventral body wall **E** perforated rods of dorsal papillae **F** tables of dorsal body wall and dorsal papillae **G** buttons of dorsal body wall and dorsal papillae **H** perforated rods of ventral tube feet **I** end plate of ventral tube feet. Scale bars: 50 μm (**A, I**) , 20μm (**B–H**).

1912); China, South China Sea (Liao and Clark 1995; Lane et al. 2000), Philippines, Borneo, Cocos (Keeling) Islands (Marsh 1994), Kerimba Archipelago (Mozambique) (Pearson 1910), Red Sea (Ludwig 1880), Mauritius (Ludwig 1883), Glorioso Islands (Mulochau and Conand 2008; this work), South Africa (Thandar 2008).

Discussion. The two examined specimens are very similar, except for the size of the rods of the tentacles. This is because the ossicles isolated from the tentacles of the type specimen originate from the tentacle shaft, whereas those removed from the non-type specimen originate from the tentacle tip. According to numerous observations the

length of tentacle rods diminishes from the base to the tip in many holothurians (e.g., Cherbonnier and Féral 1984; Cherbonnier 1988; Massin 1999).

Redescription of *Holothuria* (*L.*) *lineata* based on the morphological study of a specimen from Glorioso Islands and on the lectotype specimen from Bowen (Queensland, Australia) revealed that *H. lineata* is a distinct and well-diagnosed taxon, despite earlier claims (Panning 1935; Clark 1946) to consider it as a junior subjective synonym of *H. pardalis*. Moreover, *H. pardalis* (and thus *in se H. lineata*) is often confused with closely related species such as *H. verrucosa* Selenka, 1867 and *H. insignis* Ludwig 1875. Therefore a key is presented here to show the interspecific differences between these species.

Holothuria verrucosa is characterised by fully developed tables with numerous (more than eight) peripheral holes and with the edge of the disk bearing numerous minutes spines (Cherbonnier 1980, 1988; Liao and Clark A.M., 1995; Samyn 2003) versus reduced tables in *H. lineata, H. insignis,* and *H. pardalis. Holothuria verrucosa* is also characterised by the presence of 24–30 tentacles versIus 18–20 for the three other species. The ossicle assemblage of the tube feet of *H. pardalis* are characterised by massive curved rods with 1–3 perforations at the extremities versus slender curved rods with 2–7 perforations at the extremities for the three other species. *Holothuria insignis* differs from the three other species by a majority of buttons (or pseudo buttons) being reduced to one row of perforations (see Ludwig 1875; Panning 1951, Liao and Clark 1995).

The key below allows separation of *Holothuria lineata* from the three most similar species

1	24–28 tentacles, tables fully developed with up to eight peripheral perforations ..... ***Holothuria verrucosa***
–	18–20 tentacles, tables reduced with no or low spire and few peripheral perforations **2**
2	Majority of buttons with one row of holes ..... ***Holothuria insignis***
–	Majority of buttons with two rows of holes..... **3**
3	Length of body up to 12 cm; rods of tube feet massive, curved, with 1–3 distal perforations; perforated plates of dorsal tube feet with 3–4 rows of holes. ..... ***H. pardalis***
–	Length of body up to 6 cm; rods of tube feet slender, only slightly curved, with 2–7 holes at the extremities, perforated plates of dorsal tube feet with two rows of holes ..... ***H. lineata***

Conclusion

Holothuria lineata has often been confused with other species, notably with *H. pardalis* of which it was long time considered a junior subjective synonym. In fact, Rowe (in Rowe and Gates 1995) demonstrated that the type series of *H. pardalis* contains six

specimens that need to be referred to *H. lineata*. It can thus be expected that the confusion between *H. pardalis* and *H. lineata* will also exist in the literature. Such is, for instance, the case in Rowe (1985) and Massin (1999) where the *H. pardalis* specimens should be referred to *H. lineata*.

As *H. lineata* is distinctly smaller than *H. pardalis* one could argue that the former is but a juvenile of the latter. This reasoning is, however, not upheld by the ossicle assemblage of the two species.

This confusion between species also makes that the distribution of *H. lineata* and its related species largely unknown. We expect that the present re-description will help to unveil the true identity of previously and potentially newly collected specimens in this group and as such also will reveal the actual distribution of the various species.

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Egg parasitoids of the tea green leafhopper *Empoasca onukii* (Hemiptera, Cicadellidae) in Japan, with description of a new species of *Anagrus* (Hymenoptera, Mymaridae)

Serguei V. Triapitsyn[1], Tetsuya Adachi-Hagimori[2], Paul F. Rugman-Jones[1], Adema Barry[3], Aoba Abe[4], Kazunori Matsuo[5], Kazuro Ohno[3]

1 *Department of Entomology, University of California, Riverside, California, USA* **2** *Organization for Promotion of Tenure Track, University of Miyazaki, Miyazaki, Japan* **3** *Interdisciplinary Graduate School of Agriculture and Engineering, University of Miyazaki, Miyazaki, Japan* **4** *Faculty of Agriculture, University of Miyazaki, Miyazaki, Japan* **5** *Faculty of Social and Cultural Studies, Kyushu University, Fukuoka, Japan*

Corresponding author: *Tetsuya Adachi-Hagimori* (tadachi@cc.miyazaki-u.ac.jp)

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Abstract

Fairyfly (Hymenoptera, Mymaridae) egg parasitoids of the tea green leafhopper *Empoasca* (*Matsumurasca*) *onukii* Matsuda (Hemiptera, Cicadellidae), an economically important pest in Asia of the tea plant, *Camellia sinensis*, were identified from specimens reared in Japan. Using a combination of genetic and morphological evidence, *Anagrus* (*Anagrus*) *rugmanjonesi* Triapitsyn & Adachi-Hagimori, **sp. n.**, is described and illustrated. It is shown to be different from the most similar *A. turpanicus* Triapitsyn & H*u, an* egg parasitoid of a leafhopper pest of cultivated grapes which is known from Xinjiang Uyghur Autonomous Region in China. Mitochondrial and nuclear ribosomal DNA sequence data provide clear evidence for the separation of *A. rugmanjonesi* from *A. turpanicus* and other members of the *Anagrus incarnatus* Haliday species complex. A key to females of the Japanese species of *Anagrus* Haliday is given. Two other species of Mymaridae, *Arescon enocki* (Subba Rao & Kaur) and *Stethynium empoascae* Subba Rao, are also identified, albeit the latter one only tentatively. Both latter taxa are newly recorded from Japan, and *E. onukii* represents their new host association.

Keywords
Anagrus rugmanjonesi, *Arescon enocki*, egg parasitoid, molecular identification, *Stethynium empoascae*, taxonomy, tea pest

Introduction

The tea green leafhopper, *Empoasca* (*Matsumurasca*) *onukii* Matsuda (Hemiptera, Cicadellidae) (Fig. 1) is one of the major pests of tea plants in Japan and also in mainland China and Taiwan where it has been commonly misidentified as *Empoasca vitis* (Göthe) and *Jacobiasca formosana* (Paoli) (or as *Empoasca formosana* Paoli), respectively (Qin et al. 2015). Adults and nymphs of *E. onukii* cause leaf vein reddening, leaf margin yellowing, leaf curling, stunted shoot growth, and leaf drop, which results in economic losses of up to 33% (Xu et al. 2005). Eggs of *E. onukii* are laid singly, embedded in the soft tissues of tea bushes, such as veins of leaves and tender stems (Takagi 1978).

In Japan, tea green leafhoppers have developed resistance to the insecticides (Ozawa et al. 2009) used intensively against this pest. Thus, development of alternative control methods is desirable. Egg parasitoids offer one potential alternative for regulating tea green leafhopper populations. Takagi (1978) found mymarid wasps (Hymenoptera, Mymaridae), known as fairyflies in English, in tea fields in Japan, and later, Ojima et al. (2010) provided data on the population dynamics of three species parasitizing eggs of *E. onukii* in tea plantations in Kochi Prefecture. However, biological control-based integrated pest management (IPM) using these egg parasitoids has not yet been established.

Unfortunately, voucher specimens of the study by Takagi (1978) could not be located, and those of Ojima et al. (2010) were lost (I. Ojima personal communication). Thus, as the first step towards establishment of biological control-based IPM using egg parasitoids, we collected fairyflies in organic tea fields and identified them both morphologically and genetically.

Materials and methods

Specimen collection

Tea shoots were collected from three organic tea fields in Takaoka (Takaoka, fields 4, 5, 6), Miyazaki City on October 10, 17, and 25, and in one organic tea field in Kitakata (Kita, field 1), Nobeoka City, Miyazaki Prefecture, on October 20, 2017. All tea plants belonged to variety 'Yabukita'. In each field, 75–95 new shoots (15–20 cm length) were collected, put into plastic bags, kept in a cooler box containing ice, and transported to the Laboratory of Applied Entomology, University of Miyazaki, Miyazaki. The shoots were then transferred to two different container sets for observing either eclosion of the nymphs of tea green leafhoppers or emergence of egg parasitoid adults. The first container type consisted of plastic bottles covered with black opaque plastic

Figure 1. *Empoasca* (*Matsumurasca*) *onukii* adult feeding on a tea leaf (Miyazaki Prefecture, Kyushu Island).

film. The bottom of the bottle was cut off and replaced with the lid of a candy bottle. The latter was filled with a wetted garden sponge into which 20 tea shoots with one leaf per shoot were inserted. A transparent plastic test tube was screwed on the top of the plastic bottle. This system allowed for observation and collection of the emerged wasps from tea shoots through the test tube, as they are attracted to light. The second set of containers consisted of test tubes. A tea shoot without leaves was inserted into a small cut of wet garden sponge. The shoot inserted into wet garden sponge was put into a test tube and sealed with parafilm. The emerged wasps were collected every 24 hours and were provided with honey solution until they died naturally. The dead wasps were collected, labeled, placed in 99.5% ethanol and stored at –20 °C until they were shipped to the first author. These specimens were used both for molecular analyses and taxonomic studies (as type material of the new species described below).

Taxonomic studies

Morphological identifications of the *Anagrus* sp., made by the first author, were based mainly on females because males of many species of *Anagrus* Haliday are often similar.

Results of the genetic analysis were key in determining the separation of the new species of *Anagrus* from *A. turpanicus* Triapitsyn & Hu from Xinjiang Uyghur Autonomous Region in China; this species is an egg parasitoid of a leafhopper pest of culti-

vated grapes, *Arboridia kakogawana* (Matsumura) (Hu and Triapitsyn 2016), which is the most similar based on morphology of both sexes. The genetic analysis was also useful to separate the new species from other members of the *Anagrus incarnatus* Haliday species complex (Triapitsyn et al. 2018, 2019).

For the taxonomic description of the new species, the morphological terms of Gibson (1997) and Triapitsyn (2015) were used. All measurements (as length or length: width for the wings) are given in micrometres (μm). Abbreviations used in the description and key are:

F funicle segment of the female antenna or flagellomere of the male antenna;
mps multiporous plate sensillum or sensilla on the antennal flagellar segments (= longitudinal sensillum or sensilla, or sensory ridge(s)).

Specimens from ethanol were dried using a critical point drier, then point-mounted and labeled. Selected specimens were dissected and slide-mounted in Canada balsam. Slide mounts were examined under a Zeiss Axioskop 2 plus compound microscope (Carl Zeiss Microscopy, LLC, Thornwood, New York, USA) and photographed using the Auto-Montage system (Syncroscopy, Princeton, New Jersey, USA). Photographs were retouched where necessary using Adobe Photoshop (Adobe Systems, Inc., San Jose, California, USA).

Specimens examined are deposited in the collections with the following acronyms:

BLKU Biosystematics Laboratory, Faculty of Social and Cultural Studies, Kyushu University, Fukuoka, Japan;
UCRC Entomology Research Museum, Department of Entomology, University of California, Riverside, California, USA.

DNA extraction, amplification, and sequencing

DNA was extracted from two individual female wasps using the "HotSHOT" method of Truett et al. (2000), in a total volume of 80 μL. This non-destructive method allowed for the recovery and slide-mounting of each specimen following extraction; each slide was then labeled with the assigned P. F. Rugman-Jones' primary molecular voucher PR number and UCRC database UCRC ENT number. For reasons described below, DNA was also extracted from one male (PR18-486) using a Chelex[100] method described by Stouthamer et al. (1999). This specimen was destroyed by grinding and is listed below under "Other (non-type) material examined". Two "preliminary" specimens of the same species of *Anagrus* were also subject to a destructive extraction protocol in Japan.

The polymerase chain reaction (PCR) was employed in an attempt to amplify the "barcoding" region of the mitochondrial cytochrome c oxidase subunit I gene (COI) using LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3'; Folmer et al. 1994), as described

in Rugman-Jones et al. (2012). This primer combination has previously proved good for use with HotSHOT-extracted specimens of *Anagrus* (e.g. Triapitsyn et al. 2018, 2019). However, in this instance, amplification of COI from the HotSHOT-extracted specimens failed for these and several alternative primer combinations (data not shown). In contrast, amplification of COI from the Chelex^{100}-extracted specimen, and the two "preliminary" specimens extracted in Japan, worked fine. Reactions were performed in 25 μL volumes on a Mastercycler ep gradient S thermocycler (Eppendorf North America Inc., New York, New York, USA) and amplification was confirmed by gel electrophoresis.

In a separate PCR, the internal transcribed spacer 2 (ITS2) region of nuclear ribosomal RNA (rRNA) was amplified for all 3 specimens extracted by PRJ (HotSHOT- and Chelex^{100}-extractions) using the primers, 58SF (5'-GTGAACTGCAGGACACATGAAC-3') (Porter and Collins 1991) and ITS4 (5'-TCCTCCGCTTATTGATATGC-3') (White et al. 1990), as described in Morse et al. (2016).

All PCR products were cleaned using a DNA Clean & Concentrator™-5 kit (Zymo Research Corporation, Irvine, California, USA) and direct sequenced in both directions at the Institute for Integrative Genome Biology, University of California at Riverside. The parity of forward and reverse reads was checked using SEQUENCHER 4.9 (Gene Codes Corporation, Ann Arbor, Michigan, USA) and priming regions were removed manually in BioEdit version 7.0.5.3 (Hall 1999). The online tool, EMBOSS Transeq (Rice et al. 2000) was used to translate the protein coding COI sequence into its amino acid chain, confirming the absence of indels and pseudogenes. All sequences were deposited in GenBank (Benson et al. 2008).

Genetic analysis

Representative COI sequences previously obtained by Triapitsyn et al. (2018, 2019) for members of the *incarnatus* species complex (and associated out-group taxa) were combined with the current COI data. The sequence data was subsequently aligned using MAFFT version 7.050 (Katoh and Standley 2013) and the Q-INS-i algorithm with default settings. The aligned COI dataset contained 23 terminal taxa (including outgroups), 587 nucleotide positions, and no gaps. Genetic variation among our sequences was estimated by calculating uncorrected p-distances between all possible sequence pairs, using MEGA version 6 (Tamura et al. 2013). All ambiguous positions were removed for each sequence pair. A neighbor-joining (NJ) tree based on those p-distances was subsequently constructed, again using MEGA. Branch support was estimated using a bootstrap procedure with 1000 replicates.

As phylogenetic inference from ITS2 is typically problematic due to large interspecific differences that make alignment of this region difficult and somewhat ambiguous, ITS2 sequences were examined "by eye" to corroborate the status of our specimens as a single species, and to compare them with other *Anagrus* species by using a BLAST search of the NCBI database.

Results

Taxonomy

***Anagrus* (*Anagrus*) *rugmanjonesi* Triapitsyn & Adachi-Hagimori, sp. n.**
http://zoobank.org/26BD44A5-87B3-4AD9-968A-83B9A2B0DECC
Figures 2–5

?*Anagrus* sp.: Takagi 1978: 101–102 (egg parasitoid of tea green leafhopper and its population dynamics in Japan).

Mymaridae sp. A (resembling *Anagrus*): Ojima et al. 2010: 38–41 (egg parasitoid of tea green leafhopper and its population dynamics in Kochi Prefecture, Shikoku Island, Japan), 43–44 (photographs).

Type material. Holotype female, deposited in BLKU, on slide (Fig. 2b) labeled: 1. "JAPAN: Miyazaki Prefecture (Kyushu I.), Miyazaki City, Takaoka Takaoka5 field, parasitized eggs of *Empoasca onukii* Matsuda collected 17.x.2017, parasitoids emerged 28.x.2017, A. Barry. On tea, *Camellia sinensis*. Vial #75"; 2. "Mounted by V. V. Berezovskiy 2018 in Canada balsam"; 3. [magenta] "*Anagrus* (*Anagrus*) *rugmanjonesi* Triapitsyn & Adachi-Hagimori HOLOTYPE ♀"; 4. "Det. by S. V. Triapitsyn 2018"; 5. [barcode database label/unique identifier] "UCRC [bold] UCRC_ENT 00504791". The holotype (Fig. 3a) is in good condition, complete.

Paratypes. JAPAN, Kyushu Island, Miyazaki Prefecture (from parasitized eggs of *E. onukii* on tea plant, *Camellia sinensis*): Miyazaki City, Takaoka: Takaoka 4 field, collected 17.x.2017, emerged 26.x.2017, A. Abe (vial #18) [1 female on point, BLKU (UCRC_ENT 00504790) and 1 female on slide, UCRC (molecular voucher PR18-238, UCRC_ENT 00506187)]; Takaoka 5 field, collected 17.x.2017, emerged 26.x.2017, A. Barry (vial #73) [1 female on point, UCRC (UCRC_ENT 00504789)]; Takaoka 5 field, collected 17.x.2017, emerged 31.x.2017, A. Barry (vial #71) [1 male on point, UCRC (UCRC_ENT 00504788)]; Takaoka 6 field, collected 17.x.2017, emerged 24.x.2017, A. Abe (vial #11) [1 female on slide, BLKU (UCRC_ENT 00506185)]; Takaoka 6 field, collected 17.x.2017, emerged 25.x.2017, A. Abe (vial #12) [1 male on slide, BLKU (UCRC_ENT 00506184)]. Nobeoka City, Kitakata, Kita 1 field: collected 20.x.2017, emerged 27.x.2017, A. Abe (vial #32) [1 female on slide, UCRC (molecular voucher PR18-239, UCRC_ENT 00506188)]; collected 20.x.2017, emerged 26.x.2017, A. Barry (vial #38) [1 female on slide, UCRC (UCRC_ENT 00506186)]; collected 20.x.2017, emerged 27.x.2017, A. Barry (vial #37) [1 male on slide, UCRC (UCRC_ENT 00506183)].

Other (non-type) material examined. JAPAN, Kyushu Island, Miyazaki Prefecture (from parasitized eggs of *E. onukii* on tea plant, *Camellia sinensis*): Miyazaki City, Takaoka: Takaoka 4 field, collected 10.x.2017, emerged 12.x.2017, A. Abe (vial #15) [1 female in ethanol, UCRC]; Takaoka 4 field, collected 10.x.2017, emerged

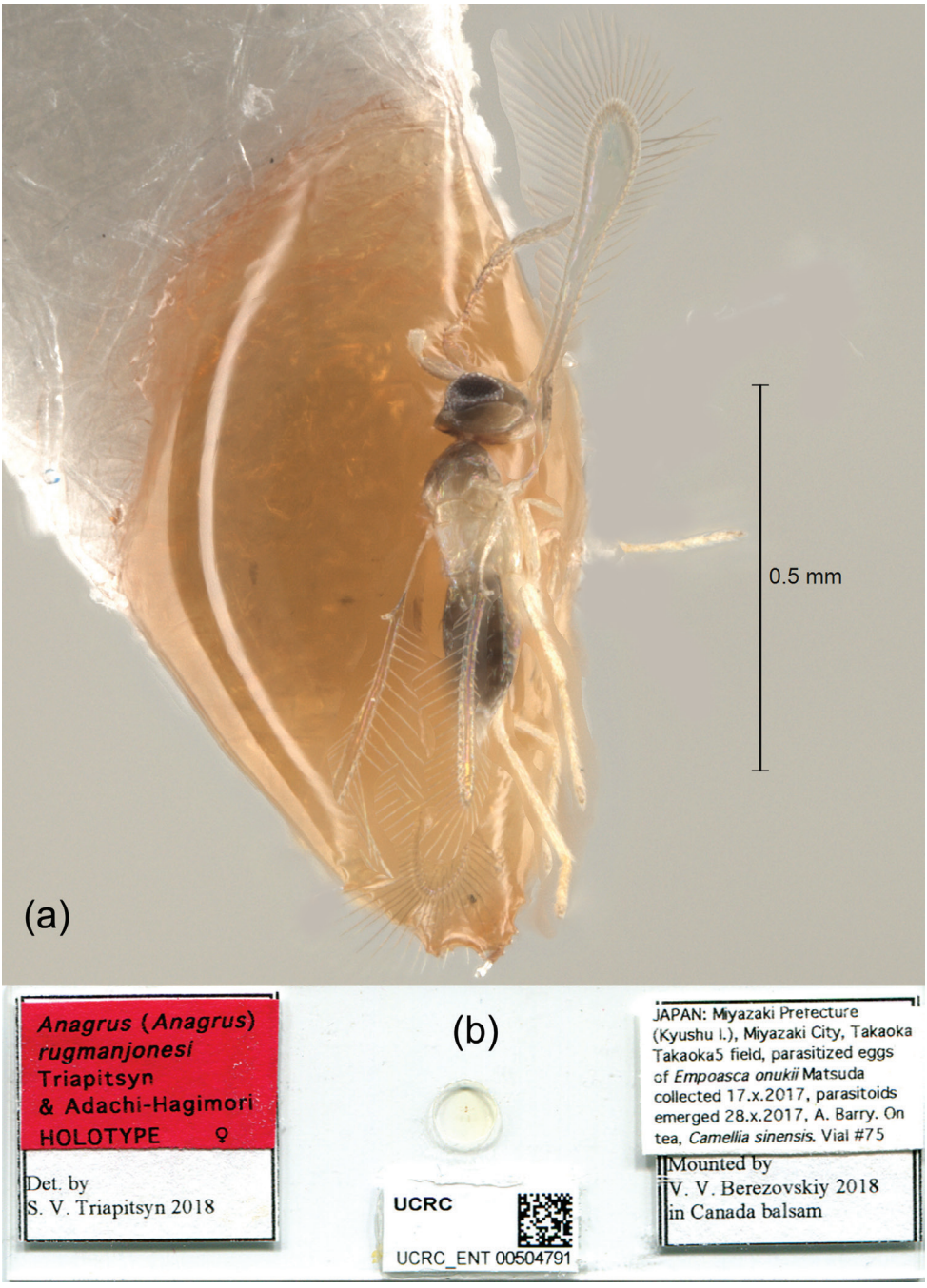

Figure 2. *Anagrus rugmanjonesi* sp. n. female: **a** habitus of dry-mounted specimen (paratype from Takaoka, Miyazaki City, Miyazaki Prefecture, Kyushu Island) **b** slide (holotype).

19.x.2017, A. Abe (vial #17) [1 male in ethanol, UCRC]; Takaoka 4 field, collected 17.x.2017, emerged 26.x.2017, A. Abe (vial #16) [1 male in ethanol, UCRC]; Takaoka 5 field, collected 25.x.2017, emerged 31.x.2017, A. Barry (vial #72) [1 male, destroyed for DNA extraction, PR18-486]. Nobeoka City, Kitakata, Kita 1 field, collected 20.x.2017, emerged 1.xi.2017, A. Abe (vial #34) [1 female in ethanol, UCRC].

Diagnosis. The new species is a member of the *incarnatus* species group of the *Anagrus* (*Anagrus*) as defined by Chiappini et al. (1996), and its *A. incarnatus* species complex, studied by Triapitsyn et al. (2018). Female antenna (Fig. 3b) with F2 not the longest funicular segment (usually F4 is or, sometimes, F6); mps on F4 (1), F5 (1 or 2), F6 (2), and clava (5); midlobe of mesoscutum without adnotaular setae (Figs 4d, 5b); fore wing disc sometimes with a distinct, but small subapical bare area (Fig. 4b) but often this bare area is either somewhat indistinct (Fig. 4a) or absent (Fig. 4c); ovipositor 2.3–2.5× length of protibia.

Morphologically, *A. rugmanjonesi* is most similar to the Palaearctic species *A. turpanicus*, to which its female specimens with a more or less distinct bare area on the fore wing disc key in Li et al. (2018). Both taxa have F2 of the female antenna not the longest funicular segment whereas in the other members of the *A. incarnatus* species complex it is the longest one (Triapitsyn 2015; Hu and Triapitsyn 2016; Triapitsyn et al. 2018). In *A. turpanicus*, however, the mesosoma is mostly yellowish brown except anterior half or so of mesoscutum is brown and frenum is yellowish white (Hu and Triapitsyn 2016), whereas in *A. rugmanjonesi* the scutellum and mesosoma (laterally, except the pronotum) are contrastingly white (Fig. 2a). Also, in *A. rugmangonesi* the clava is at most as long as the combined length of F5 and F6 whereas it is always longer than that in *A. turpanicus*. The fact that the two species also substantially differ genetically (Fig. 7) provides a good justification for their differentiation as two separate entities. In Li et al. (2018), those specimens of *A. rugmanjonesi* that lack a more or less distinct bare area on the fore wing disc key to *Anagrus nilaparvatae* Pang & Wang, a well-known egg parasitoid of rice planthoppers (Hemiptera, Delphacidae) and leafhoppers in Asia. The latter taxon was recently synonymized under *Anagrus incarnatus*, and F2 of its female antenna is always the longest funicular segment (Triapitsyn et al. 2018). A key to females of the Japanese species of *Anagrus* is provided below, as the previous key by Sahad and Hirashima (1984) is outdated.

Description. Female (holotype and paratypes). Body length of dry-mounted, critical point-dried paratypes 400–460 μm, and of the slide-mounted paratypes 560–590 μm. Body (Figs 2a, 3a) mostly brown to dark brown except face, gena, and propodeum light brown and scutellum and mesosoma laterally (except pronotum) white; posterior half or so of mesoscutum and apex of gaster often light brown to off-white; scape, pedicel and F1 pale to light brown, remaining funicular segments light brown, and clava brown; legs mostly pale to light brown, wings hyaline. Antenna (Fig. 3b) with scape 2.9–3.8× as long as wide, with cross-ridges, 1.9–2.2× length of pedicel; F1 a little longer than wide, about half of pedicel length; F2 at least slightly shorter than following funicular segments, F4 usually the longest funicular segment (except sometimes F6 the longest); mps on F4 (1); F5 (1 or 2), and F6 (2); clava with 5 mps, 2.8–3.3× as long as wide, either as long as combined length of F5 and

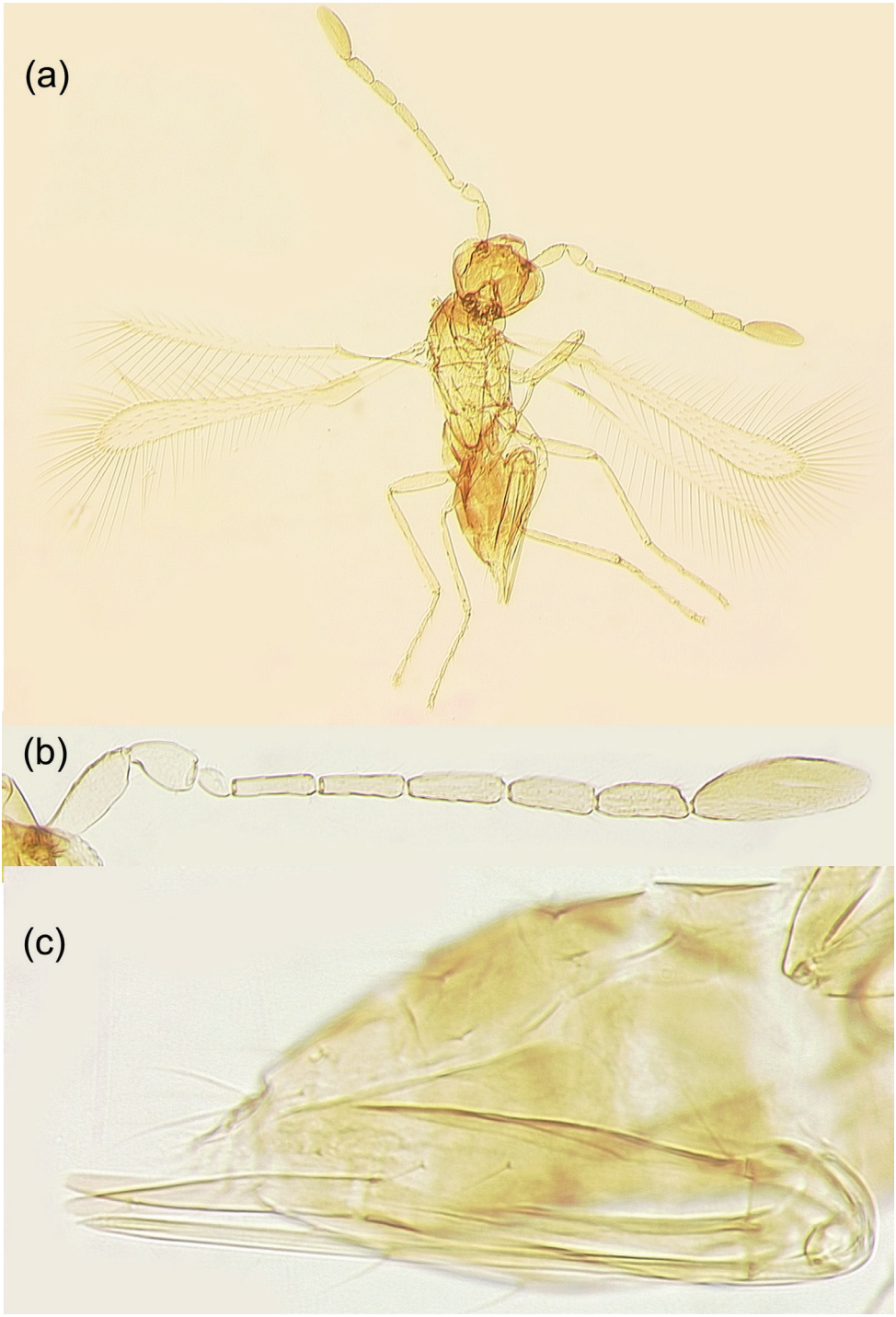

Figure 3. *Anagrus rugmanjonesi* sp. n. female: **a** holotype habitus **b** holotype antenna **c** metasoma (paratype from Kitakata, Nobeoka City, Miyazaki Prefecture, Kyushu Island).

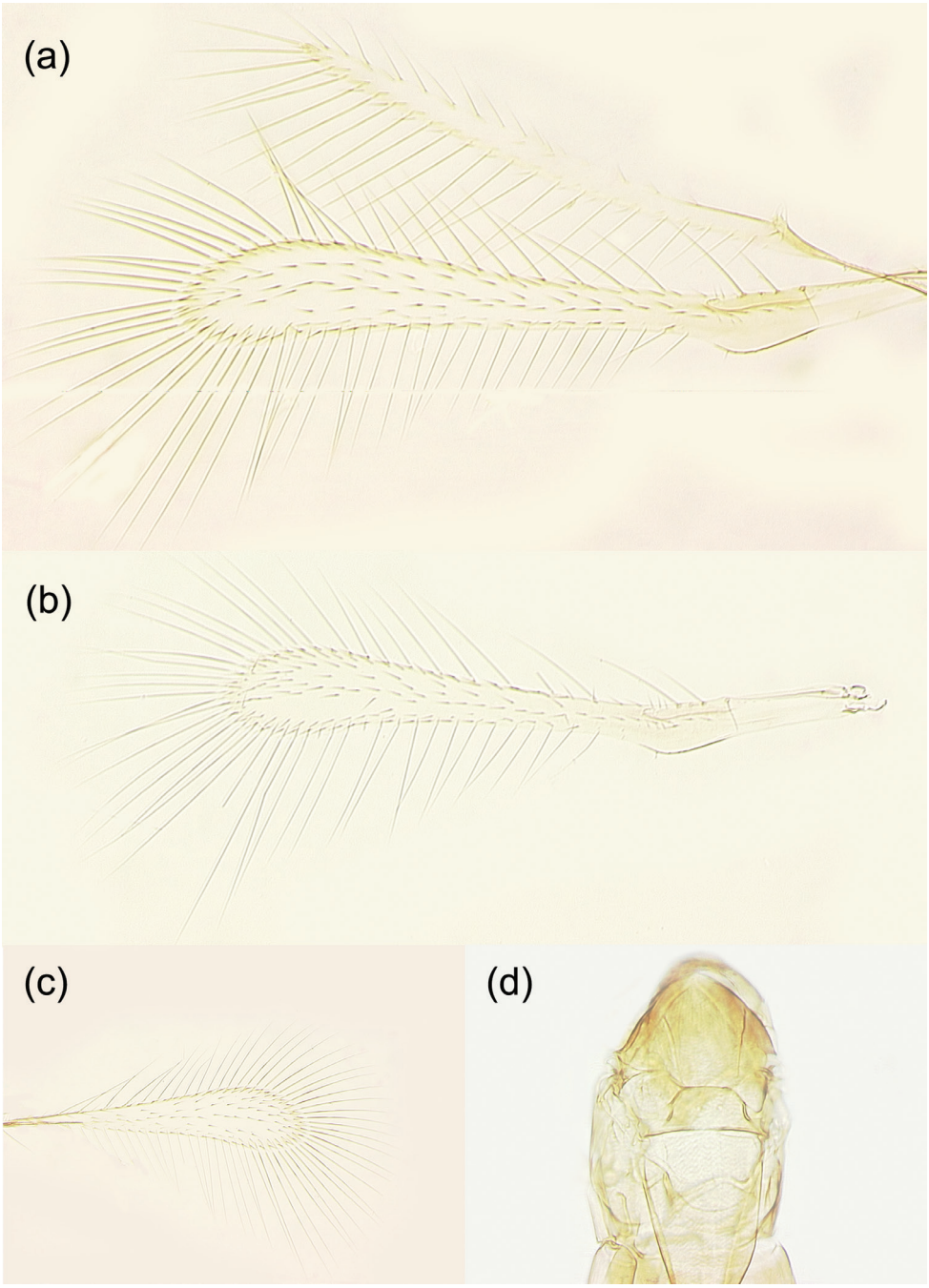

Figure 4. *Anagrus rugmanjonesi* sp. n. female: **a** fore and hind wings (holotype) **b** fore wing (paratype from Takaoka, Miyazaki City, Miyazaki Prefecture, Kyushu Island) **c** fore wing (paratype from Kitakata, Nobeoka City, Miyazaki Prefecture, Kyushu Island) **d** mesosoma (paratype from Takaoka).

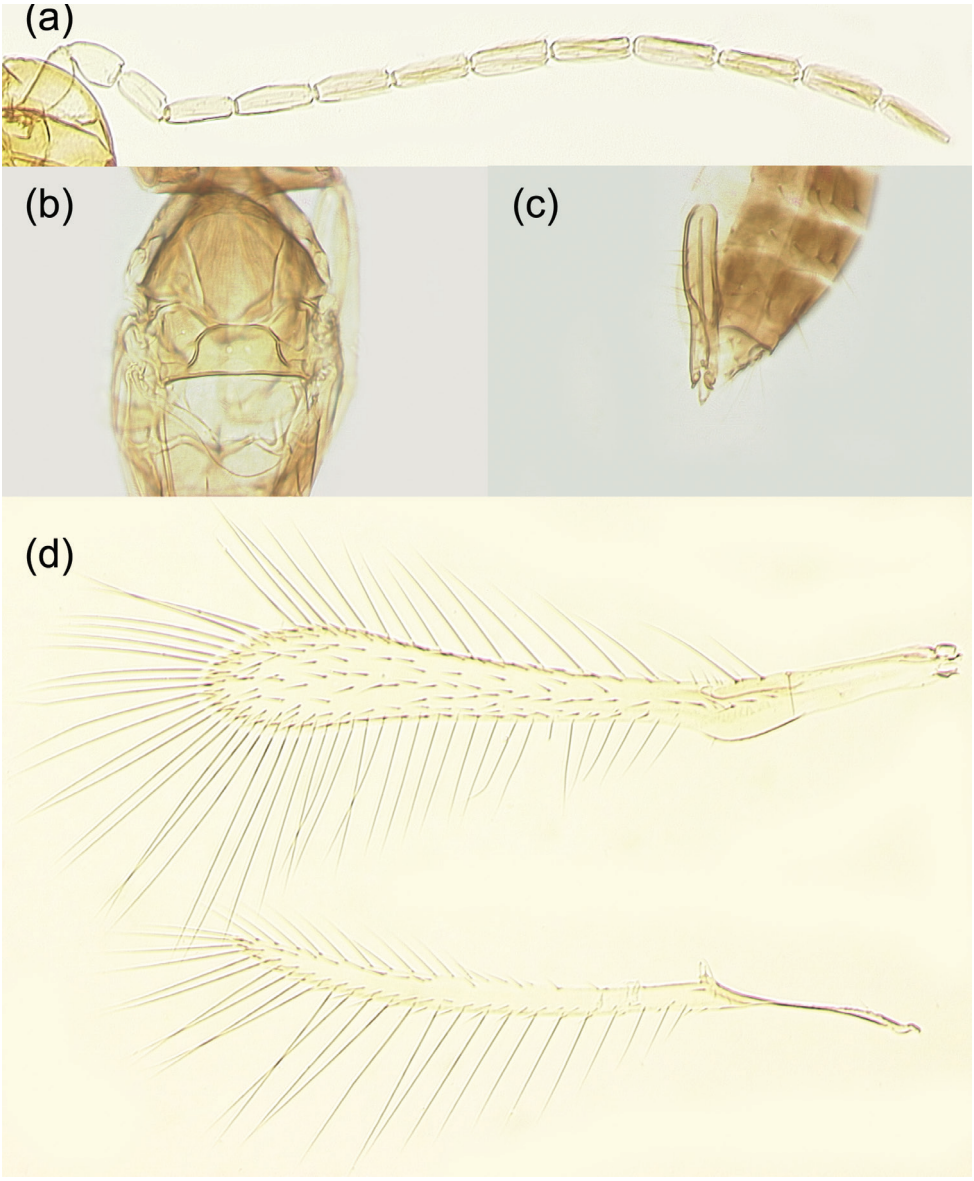

Figure 5. *Anagrus rugmanjonesi* sp. n. male (paratypes from Miyazaki Prefecture, Kyushu Island, Japan: **a–c**, Kitakata, Nobeoka City; d, Takaoka, Miyazaki City): **a** antenna **b** mesosoma **c** genitalia **d** fore and hind wings.

F6 or slightly shorter. Midlobe of mesoscutum without adnotaular setae (Fig. 4d). Fore wing (Fig. 4a–c) 7.0–8.0× as long as wide, longest marginal seta 2.6–2.9× maximum wing width; distal macrochaeta 1.6–1.7× length of proximal macrochaeta; disc with several rows of setae in addition to admarginal rows of setae (1 complete row originating behind apex of venation and 3 or 4 irregular rows in the broadest part of disc), sometimes leaving a distinct, but small subapical bare area at posterior margin (Fig. 4b) but often this bare area either somewhat indistinct (Fig. 4a) or absent (Fig. 4c). Hind wing (Fig. 4a) 22–24× as long as wide, longest marginal seta 6.0–7.0× maximum wing width; disc mostly bare except for an incomplete row of setae along anterior margin and a compete row of setae along posterior margin. Ovipositor (Fig. 3c) extending anteriorly almost to mesophragma in slide-mounted specimens and exserted a little beyond apex of gaster posteriorly (by 0.12–0.15× total ovipositor length). Second valvifers (= external plates of ovipositor), e.g., Chiappini et al. (1996), each with 3 setae (Fig. 3c). Ovipositor 2.3–2.5× length of protibia (2.35× in the holotype).

Measurements (μm) of the holotype (as length or length: width). Body: 535; mesosoma 190; gaster 264; ovipositor 245. Antenna: scape 70; pedicel 36; F1 18; F2 42; F3 45; F4 52; F5 45; F6 48; clava 97. Fore wing 511: 64; longest marginal seta 173. Hind wing 476: 21; longest marginal seta 127.

Male (paratypes). Body length of the slide-mounted paratypes 560–585 mm. Body color mostly as in female except entire flagellum brown. Antenna (Fig. 5a) with scape 2.4–2.7× as long as wide, F1 at least a little shorter than following flagellomeres. Fore wing 7.2–7.6× as long as wide, with or without (Fig. 5d) a more or less bare area in the broadest part. Genitalia (Fig. 5c) length 124–127 μm.

Etymology. This new species is named by the first author in honor of his colleague and one of the co-authors of this communication, Paul F. Rugman-Jones, whose contributions towards determination of the identities of the nominal taxa within the *Anagrus incarnatus* species complex using molecular methods and genetic analyses have been invaluable.

Distribution. Palaearctic region: Japan.

Host. Cicadellidae: *Empoasca* (*Matsumurasca*) *onukii* Matsuda.

Biology. In eggs of *E. onukii* on tea plants, *A. rugmanjonesi* was observed to develop as a solitary endoparasitoid (Ojima et al. 2010). Takagi (1978) monitored population dynamics of *A. rugmanjonesi* (as *Anagrus* sp.) in a tea plantation by using sticky suction traps. The dynamic curve indicated that *A. rugmanjonesi* was a multivoltine species and was most abundant in September. The study site of Takagi (1978) was not mentioned but is known to be the former Kanaya Town, Shizuoka Prefecture, Japan (K. Takagi personal communication), which is now part of Shimada City.

Comments. The photographs of "Mymaridae sp. A" provided in Ojima et al. (2010) leave no doubt that their specimens from Kochi Prefecture, Shikoku Island belonged to both sexes of *Anagrus rugmanjonesi* n. sp.

Key to females of the Japanese species of *Anagrus*

1 Ocelli on a stemmaticum **3**
– Ocelli not on a stemmaticum (subgenus *A.* (*Anagrella*) Bakkendorf) **2**
2 F2 approximately 1.5× F1 length ..... ***Anagrus* (*Anagrella*) *brevis* Chiappini & Lin**
– F2 at least 4.0× F1 length ..... ***Anagrus* (*Anagrella*) *hirashimai* Sahad**
3 Frenum of scutellum with triangular paramedial plates widely separated from each other; metafemur short, less than 2× trochanter length, trochantellus incision almost halfway between coxa-trochanter and femur-tibia articulations (subgenus *A.* (*Paranagrus*) Perkins) **4**
– Frenum of scutellum with triangular paramedial plates very close to each other; metafemur long, more than 2× trochanter length, trochantellus incision about 1/3 way between coxa-trochanter and femur-tibia articulations (subgenus *A.* (*Anagrus* Haliday) [sensu stricto]) **5**
4 Ovipositor projecting beyond apex of gaster by approximately 1/3 of its total length; ovipositor length: protibia length ratio at least 3.5 ..... ***Anagrus* (*Paranagrus*) *perforator* (Perkins)**
– Ovipositor not projecting or at most slightly projecting beyond apex of gaster; ovipositor length: protibia length ratio at most 2.5 ..... ***Anagrus* (*Paranagrus*) *optabilis* (Perkins)**
5 Clava with 3 mps (*atomus* species group) **6**
– Clava with 5 mps (*incarnatus* species group) **7**
6 Fore wing length: width ratio > 10 ..... ***Anagrus* (*Anagrus*) *frequens* Perkins**
– Fore wing length: width ratio < 8 ..... ***Anagrus* (*Anagrus*) *japonicus* Sahad**
7 Midlobe of mesoscutum with adnotaular setae ..... ***Anagrus* (*Anagrus*) *subfuscus* Foerster**
– Midlobe of mesoscutum without adnotaular setae **8**
8 Fore wing approximately 6.3× as long as wide ..... ***Anagrus* (*Anagrus*) *takeyanus* Gordh**
– Fore wing at least 7.0× as long as wide **9**
9 F2 the longest funicular segment ..... ***Anagrus* (*Anagrus*) *incarnatus* Haliday**
– F2 at least slightly shorter than following funicular segments ..... ***Anagrus* (*Anagrus*) *rugmanjonesi* Triapitsyn & Adachi-Hagimori, sp. n.**

***Arescon enocki* (Subba Rao & Kaur, 1959)**

Neurotes enocki Subba Rao & Kaur, 1959: 233 (illustrations), 235–237, 238 (key). Type locality: Indian Agricultural Research Institute, New Delhi, National Capital Territory of Delhi, India. Holotype female on slide [National Pusa Collection,

Division of Entomology, Indian Agricultural Research Institute, New Delhi, India (NPC)] (not examined).

Arescon enocki (Subba Rao & Kaur): Subba Rao 1966: 187–189 (description of the male, illustration of the female, distribution, host association); Triapitsyn and Berezovskiy 2003: 9 (compared with *Arescon zenit* Triapitsyn & Berezovskiy, distribution, host association); Triapitsyn 2016: 138–140 (key, taxonomic history, redescription, diagnosis, distribution, hosts, comments), 142 (illustrations).

Mymaridae sp. C: Ojima et al. 2010: 38–41 (egg parasitoid of tea green leafhopper and its population dynamics in Kochi Prefecture, Shikoku Island, Japan), 44 (photographs).

Distribution. India and Pakistan (Triapitsyn 2016), as well as Japan (new record).

Hosts. Cicadellidae: *Amrasca biguttula* (Ishida) [= *Amrasca biguttula biguttula* (Shiraki)] (Subba Rao 1966 [as *Empoasca devastans* Distant]) and *Jacobiasca lybica* (de Bergevin & Zanon) [= *Empoasca signata* (Haupt)] (Triapitsyn and Berezovskiy 2003 [as *Empoasca libyca* [sic] (de Bergevin & Zanon)]; Triapitsyn 2016), as well as *Empoasca* (*Matsumurasca*) *onukii* Matsuda (new record).

Comments. This species was redescribed and illustrated by Subba Rao (1966) and Triapitsyn (2016) based on specimens from India, so it is quite easily recognizable; particularly, Triapitsyn (2016) provided habitus digital images of both sexes of this species. The photographs of "Mymaridae sp. C" provided in Ojima et al. (2010) leave no doubt that their specimens belonged to both sexes of *A. enocki*, which thus is newly recorded from the Palaearctic region, where it is definitely an Oriental fauna element in southern Japan where tea is grown. Unfortunately, as their material was lost, we are unable to further illustrate the Japanese specimens of this species.

Stethynium ?*empoascae* Subba Rao, 1966

Figure 6

Stethynium empoascae Subba Rao, 1966: 189, 191, plate V [the figures are mislabeled as "*Lymaenon empoascae*"]. Holotype female, Delhi, India [NPC] (not examined).

Stethynium triclavatum Enock: Huber 1987: 829 (synonymy).

Stethynium empoascae Subba Rao: Triapitsyn 2002: 10–11 (resurrection as a valid species, taxonomic history, diagnosis, distribution, hosts, comments).

Mymaridae sp. B (resembling *Anagrus*): Ojima et al. 2010: 38–41 (egg parasitoid of tea green leafhopper and its population dynamics in Kochi Prefecture, Shikoku Island, Japan), 44 (photographs).

Material examined. JAPAN, Kyushu Island, Miyazaki Prefecture, Nobeoka City, Kitakata, Kita 1 field (from parasitized eggs of *E. onukii* on tea plant, *Camellia sinensis*): collected 20.x.2017, emerged 27.x.2017, A. Abe [1 female, UCRC]; collected 20.x.2017, emerged 23.x.2017, A. Barry [1 female, UCRC]; collected 20.x.2017, emerged 30.x.2017, A. Barry [2 females, BLKU, UCRC]; collected 20.x.2017, emerged

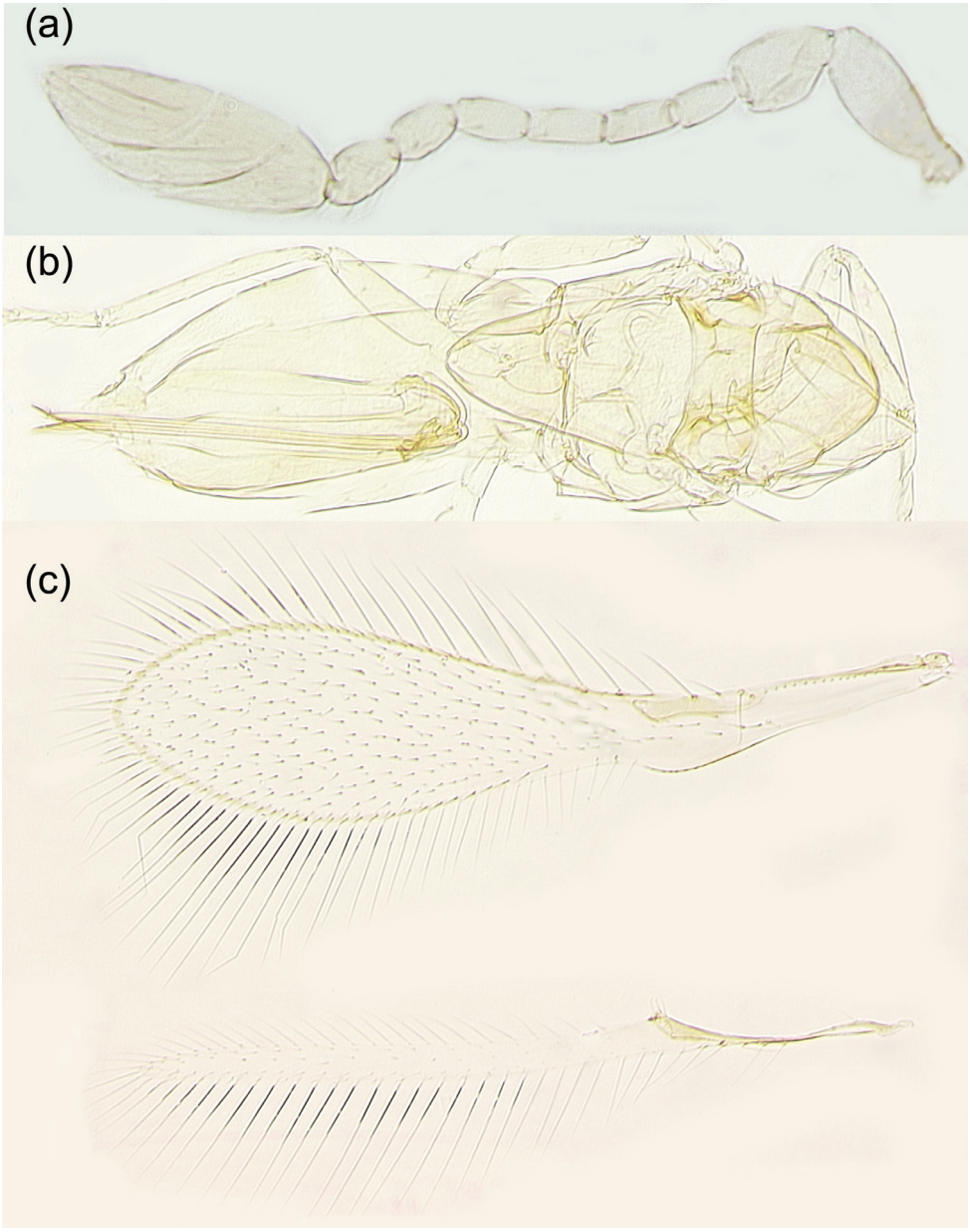

Figure 6. *Stethynium empoascae* female (from Kitakata, Nobeoka City, Miyazaki Prefecture, Kyushu Island): **a** antenna **b** mesosoma and metasoma **c** fore and hind wings.

31.x.2017, A. Barry [1 female, UCRC]; collected 20.x.2017, emerged 1.xi.2017, A. Abe [1 female, UCRC].

Distribution. Australia (Queensland) (Triapitsyn 2002), India (Subba Rao 1966), and Japan (new record).

Hosts. Cicadellidae: *Amrasca biguttula* (Ishida), *Austroasca alfalfae* (Evans), ?*Empoasca* sp., and *Jacobiasca lybica* (de Bergevin & Zanon) (Triapitsyn 2002), as well as *Empoasca* (*Matsumurasca*) *onukii* Matsuda (new record).

Comments. The photographs of "Mymaridae sp. B" provided in Ojima et al. (2010) leave no doubt that their specimens belonged to both sexes of a *Stethynium* sp., which almost certainly were conspecific with ours from the same genus.

As discussed by Triapitsyn (2002), *S. empoascae* is extremely similar morphologically to usually lighter-colored specimens of *Stethynium triclavatum* Enock to the extent that it may be impossible to distinguish them in some countries (like China, Egypt, India, Japan, Nepal, Pakistan, etc.) where both species can potentially occur. Yet, females of *S. empoascae* from Australia and India, which could be a different, more subtropical and tropical species, seem to be slightly different from the majority of the European and North American specimens of *S. triclavatum*, which supposedly occurs in the countries with a more temperate climate (Triapitsyn 2002). Ultimately, molecular studies comparing freshly preserved specimens from Australia, Europe, India, Japan, and North America (now lacking) would need to be conducted to confirm separation of these two nominal species or, otherwise, provide genetic evidence of their possible conspecificity. At this point, however, we can only tentatively assign our specimens to *S. empoascae* based on some of the very minor morphological features mentioned in Triapitsyn (2002) as well as the fact that they were collected in Japan on the two islands with a subtropical climate. To facilitate recognition of this species, we provide illustrations of its female antenna (Fig. 6a), mesosoma and metasoma (Fig. 6b), and a pair of wings (Fig. 6c).

Molecular analyses

Sequences of the COI gene provided strong evidence that *A. rugmanjonesi* is distinct from *A. turpanicus* and other members of the *A. incarnatus* species complex. Three COI haplotypes were identified for *A. rugmanjonesi*, with maximum 1.9% divergence (based on uncorrected p-distances) among those haplotypes (GenBank accessions MK544853-MK544855; Fig. 7). All substitutions were synonymous. In turn, *A. rugmanjonesi* was at least 5.1% divergent from all other accepted species in the *incarnatus* species group, with *A. turpanicus* being the most similar (Fig. 7). The exact relationship between *A. rugmanjonesi* and *A. turpanicus* (and indeed other species) was largely unresolved, with weak branch support towards the base of the NJ tree (Fig. 7).

The ITS2 sequences of the three PRJ-extracted specimens were each 603 bp long and identical, confirming them as a single species (GenBank accessions MK564750-MK564752). A BLAST search revealed no match with anything currently in the GenBank database; the closest accessions again belonging to *Anagrus turpanicus* (MK024909-MK024911). A MAFFT alignment of our sequences with those of *A. turpanicus* resulted in a matrix with many substitutions and several sizable indels, resulting in a difference in length of approximately 40 bp.

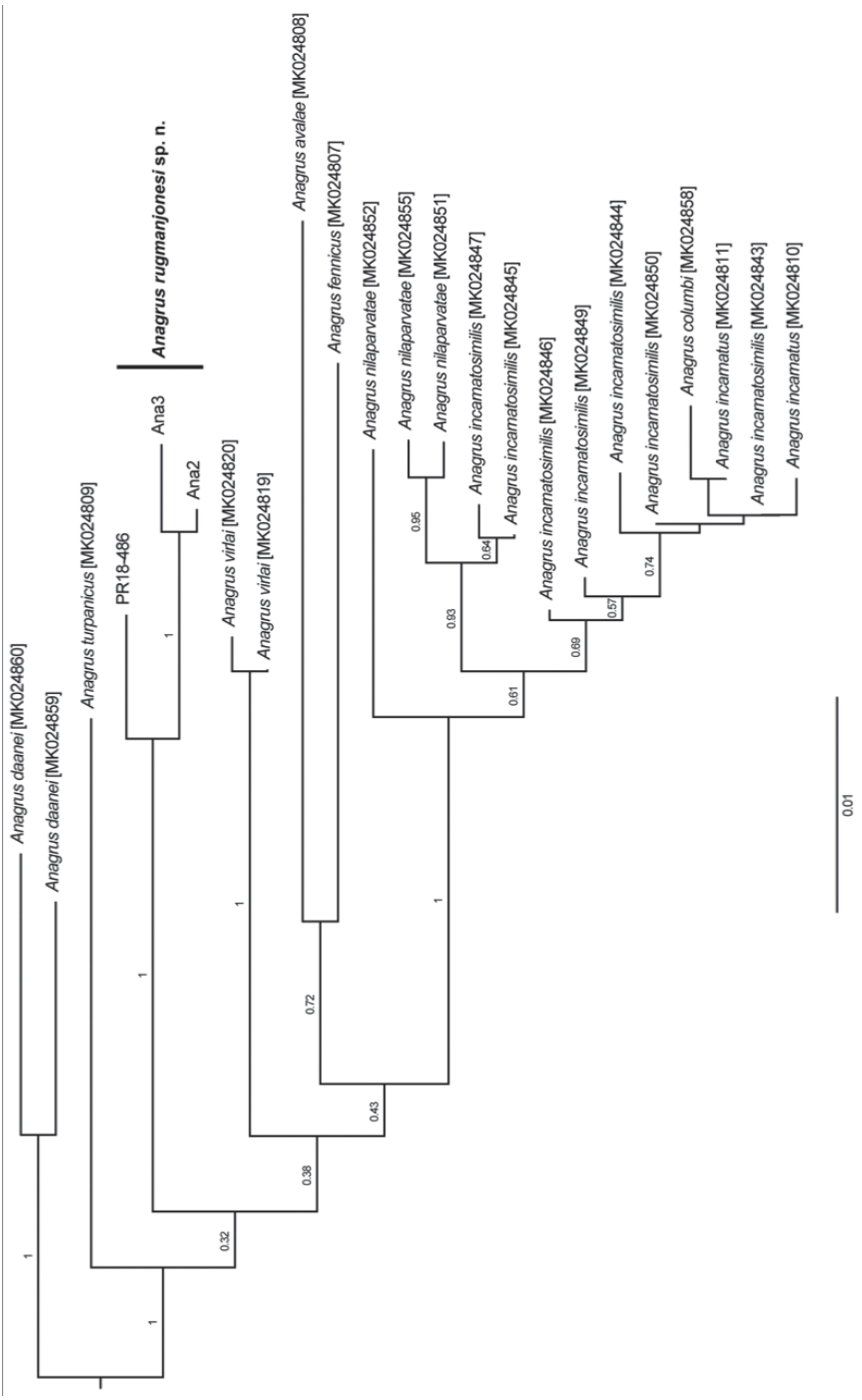

Figure 7. Relationship of *Anagrus rugmanjonesi* sp. n. with other member of the *A. incarnatus* species complex, based on a 587 bp fragment of COI. Optimal unrooted NJ tree with the sum of branch length = 0.27005784. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1000 replicates) are shown next to the branches and the tree is drawn to scale, with branch lengths indicating uncorrected p-distance.

Discussion

This study further confirms the effectiveness of simple molecular techniques for separating morphologically similar species, in this case *A. rugmanjonesi*, *A. turpanicus*, and other members of the *A. incarnatus* species complex (Fig. 7). Description of *A. rugmanjonesi* would be difficult based solely on morphology because of its close morphological similarity to *A. turpanicus*. The convincing molecular data confirms that two species are involved. Their separation also makes sense from the habitat point of view, the latter species being an egg parasitoid of a leafhopper pest of grapevines in a very hot and dry environment of a desert oasis in Xinjiang Uyghur Autonomous Region of China. Morphologically, however, they are clearly two sister species, and that is also corroborated by the genetic data presented herein.

Lin (1981) reported one undescribed species of *Megaphragma* Timberlake (Hymenoptera, Trichogrammatidae) as an egg parasitoid of *E. onukii* (as *Empoasca formosana* Paoli) on tea plant in Taiwan, but that record was obviously erroneous, likely due to an inadequate rearing method, because members of this genus are known to be egg parasitoids of thrips (Thysanoptera).

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RESEARCH ARTICLE

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Revision of the genus *Emphylica* Turner, 1913 based on morphology and molecular data (Lepidoptera, Crambidae, Pyraustinae)

Kai Chen[1], Qingming Liu[1], Jianhua Jin[1], Dandan Zhang[1]

1 *State Key Laboratory of Biocontrol/The Museum of Biology, School of Life Sciences, Sun Yat-sen University, Guangzhou, Guangdong 510275, China*

Corresponding author: *Dandan Zhang* (zhangdd6@mail.sysu.edu.cn)

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Abstract

Moths of the genus *Emphylica* Turner, 1913 resemble species of *Achyra* Guenée, 1849, *Loxostege* Hübner, 1825 and *Sitochroa* Hübner, 1825 in having a conical frons. In order to examine the monophyly of *Emphylica*, and its relationship to other genera with a conical frons, a molecular phylogenetic framework is reconstructed based on sequence data of COI, 16S rRNA, 28S rRNA, EF-1α and Wg gene regions. The results robustly support the monophyly of *Emphylica*. *Achyra* + (*Loxostege* + *Sitochroa*) is in a sister position to *Emphylica*. A new species, *E. crassihamata* **sp. n.**, is described from Southern China and two new combinations, *E. diaphana* (Caradja & Meyrick, 1934), **comb. n.** and *E. cruoralis* (Warren, 1895), **comb. n.**, are proposed. An identification key based on males is provided for all *Emphylica* species. The adult habitus and genitalia of all species are figured.

Keywords

Achyra, China, conical frons, *Loxostege*, molecular phylogeny, new combinations, new species, *Sitochroa*

Introduction

Emphylica was established by Turner (1913) and remained monotypic until now, with the type species E. xanthocrossa Turner, 1913 endemic in the north of Australia. In appearance, *E. xanthocrossa* can be best distinguished from other pyraustine species by the small wingspan (less than 15 mm), the reddish brown forewing with a yellow costal spot and the characteristic conical frons.

The frons of pyraustine species is usually flat or round, seldom projecting conically. Based on current knowledge, only the Australian genus *Emphylica* Turner, the genus *Achyra* Guenée with a worldwide distribution, the mainly Holarctic genera *Loxostege* Hübner and *Sitochroa* Hübner, as well as the New World genera *Hahncappsia* Munroe, *Neohelvibotys* Munroe and *Helvibotys* Munroe have a conical frons. These genera (except *Emphylica*) were considered closely related to each other based on external characters (Munroe 1976a).

While examining pyraustine collections from southern China and Southeast Asia, *Loxostege diaphana* Caradja & Meyrick, 1934, *Pyrausta cruoralis* (Warren, 1895) and an undescribed species, all resembling *Emphylica xanthocrossa* in the conical frons and the relatively small wingspan (less than 20 mm), attracted our attention. Further studies based on the genitalic characters suggested that the two described species definitely did not belong to their current genera and these three species were closely related to *Emphylica*. In order to evaluate the generic placement of these species, the phylogenetic relationships of *Emphylica* and potentially related genera, *Achyra*, *Loxostege,* and *Sitochroa*, were studied based on genetic data. The taxonomic composition and morphology of *Emphylica* are redefined.

Material and methods

Molecular phylogenetic analysis

In total eleven species of five genera were included for molecular phylogenetic analysis (Table 1). *Pseudebulea fentoni* Butler, 1881 was chosen as the outgroup because it was considered as a basal lineage of the Pyraustinae (Zhang 2003). The New World genera *Hahncappsia* Munroe, *Neohelvibotys* Munroe and *Helvibotys* were not included in the current study because no specimens could be accessed.

Total DNA was extracted from two legs and sometimes in addition from the abdomen of the dry specimens using the TIANGEN DNA extraction kit following the manufacturer's instructions. The nucleotide sequences of two mitochondrial genes, cytochrome c oxidase subunit I (COI) and 16S ribosomal RNA (16S rRNA), and three nuclear genes, 28S ribosomal RNA (28S rRNA), Elongation factor-1 alpha (EF-1α) and Wingless (Wg) were selected for study. Primers used in this study are as follow: LCO/Nancy for COI and LepWg1/LepWg2 for Wg (Wahlberg and Wheat

Table 1. Species sampled for the molecular phylogenetic analysis.

Taxon	Voucher	Locality	GenBank accession number					References
			COI	16S	28S	EF1-α	Wg	
Pseudebulea fentoni	SYSULEP0074	Hunan	MG739570	MG739582	MG739605	MG739594	MK506279	Chen et al. 2018; present study
Emphylica crassihamata	SYSULEP0190	Guangdong	MK506732	MK506755	MK506767	MK506744	MK506728	present study
Emphylica crassihamata	SYSULEP0191	Hunan	MK506733	MK506756	MK506768	MK506745	MK506727	present study
Loxostege deliblatica	SYSULEP0200	Xinjiang	MK506734	MK506757	MK506769	MK506746	MK506726	present study
Loxostege sticticalis	SYSULEP0227	Xinjiang	MK506735	MK506758	MK506770	MK506747	MK506725	present study
Achyra massalis	SYSULEP0242	Shanxi	MK506736	MK506759	MK506771	N/A	MK506724	present study
Sitochroa verticalis	SYSULEP0257	Xinjiang	MK506737	MK506760	MK506772	MK506748	MK506723	present study
Sitochroa palealis	SYSULEP0258	Xinjiang	MK506738	MK506761	MK506773	MK506749	MK506722	present study
Emphylica diaphana	SYSULEP0263	Fujian	MK506739	MK506762	MK506774	MK506750	MK506719	present study
Emphylica diaphana	SYSULEP0264	Guangdong	MK506740	MK506763	MK506775	MK506751	MK506720	present study
Emphylica xanthocrossa	SYSULEP0307	Western Australia	MK506741	MK506764	MK506776	MK506752	MK506730	present study
Emphylica cruoralis	SYSULEP0377	Tibet	MK506742	MK506765	MK506777	MK506753	MK506721	present study
Sitochroa umbrosalis	SYSULEPT014	Fujian	MK506743	MK506766	MK506778	MK506754	MK506731	present study

2008), LR-J-12888/ LR-N-13398 for 16S rRNA (Simon et al. 2006), Oscar-6143/ Bosie-6144 for EF-1α (Hundsdöerfer et al. 2009) and 28S-f1/28S-r1 for 28S rRNA (Lee and Brown 2008). PCR cycle conditions were set to an initial denaturation of 5 min at 95 °C, 35 cycles of 30 seconds at 94 °C, 30 seconds at 48 °C (COI, Wg and 16S rRNA) or 52 °C (EF-1α, 28S rRNA) and 1 min at 72 °C for amplification, and a final extension at 72 °C for 10 min. PCR products were confirmed with 1.5% agarose gel electrophoresis in TAE buffer, then were direct-sequenced at Majorbio Bio-pharm Technology Co., Ltd (Guangzhou), utilizing the same primers used for PCR amplification.

The sequences were aligned using Clustal W (Thompson et al. 1994) in MEGA 6 (Tamura et al. 2013) with default settings. The aligned matrix was corrected by eye. Gaps were treated as missing data. Phylogenetic analyses were inferred using Bayesian inference (BI) method in MrBayes 3.2.6 (Ronquist et al. 2012) and maximum likelihood (ML) in RAxML 8.2.10 (Stamatakis 2014). BI analysis was run with independent parameters for the COI gene partition under the GTR + I model, the 16S rRNA and 28S rRNA gene partitions under the GTR + G model, the EF-1α gene partition under the K80 + I model, and the Wg gene partition under the HKY + G model as suggested by jModelTest 0.1.1 (Posada 2008). Two independent runs, each with four Markov Chain Monte Carlo (MCMC) simulations, were performed for 10 million generations sampled every 1000th generation. The first 25% trees were discarded as burn-in, and posterior probabilities (PP) were determined from remaining trees. ML analysis was executed under the GTR + G model for all gene partitions and with 1000 iterations for the bootstrap test. The pairwise Kimura 2-Parameter (K2P) distances between species were calculated from the COI gene using MEGA 6 (Tamura et al. 2013).

Morphological analysis. The specimens studied, including the types of the newly described species, are deposited in the Museum of Biology, Sun Yat-sen University, Guangzhou (**SYSBM**), except for those held at the following institutions: the Insect Collection of the College of Life Sciences, Nankai University (**NKU**), the Australian National Insect Collection (**ANIC**), and the Natural History Museum, London, United Kingdom (**NHMUK**). Slides of dissected genitalia were prepared according to the protocols of Robinson (1976) and Li and Zheng (1996). Terminology of genitalia follows Maes (1995), except for the terms "phallus" and "colliculum" for which we follow Kristensen (2003). Images of the specimens were taken using a Canon EOS 1DX camera provided with a Canon 100 mm macro lens; images of specimen of *Emphylica cruoralis* were taken using a Canon EOS 5DS R camera provided with a Canon 65 mm macro lens. The genitalia pictures were taken using a Zeiss Axio Scope.A1 in combination with a Zeiss AxioCam camera and the Axio Vision SE64 program on a Windows PC; genitalia pictures of *Emphylica cruoralis* were taken using a Zeiss Axioskop in combination with a Canon EOS 700D camera and Helicon Remote. Source images were then aligned and stacked with Helicon Focus to obtain a composite image.

Results

Phylogenetic relationships

The concatenated dataset of five genes consisted of 2873 nucleotide positions (658 for COI, 466 for 16S, 612 for 28S rRNA, 753 for EF-1α and 384 for Wg). Both BI and ML analyses of the concatenated dataset inferred congruent topologies with only subtle differences in posterior probability and bootstrap values probability (Fig. 1). The monophyly of *Emphylica* is robustly supported (PP = 1.00, BS = 92). The clade *Achyra* + (*Loxostege* + *Sitochroa*) is in a sister position to *Emphylica* with robust support (PP = 1.00).

The results of the current phylogenetic analyses support that the undescribed species (here named as *E. crassihamata* sp. n.) should be placed in *Emphylica*, and that *E. diaphana* comb. n. should be transferred from *Loxostege* to *Emphylica* and *E. cruoralis* comb. n. should be transferred from *Pyrausta* to *Emphylica*. *Emphylica xanthocrossa* and *E. crassihamata* + *E. cruoralis* form a sister group, although with low support in the ML analysis (BS = 40).

Pairwise distances of the barcoding region (COI) are given in Table 2. The genetic distances between *Emphylica* and other genera range from 8.3% (*Loxostege*) to 14.6% (*Pseudebulea*). Interspecific genetic distances within *Emphylica* range from 4.0% (*E. crassihamata* to *E. cruoralis*) to 8.3% (*E. crassihamata* to *E. diaphana*), while intraspecific genetic distances in *Emphylica* range from 0% (*E. crassihamata*) to 0.8% (*E. diaphana*).

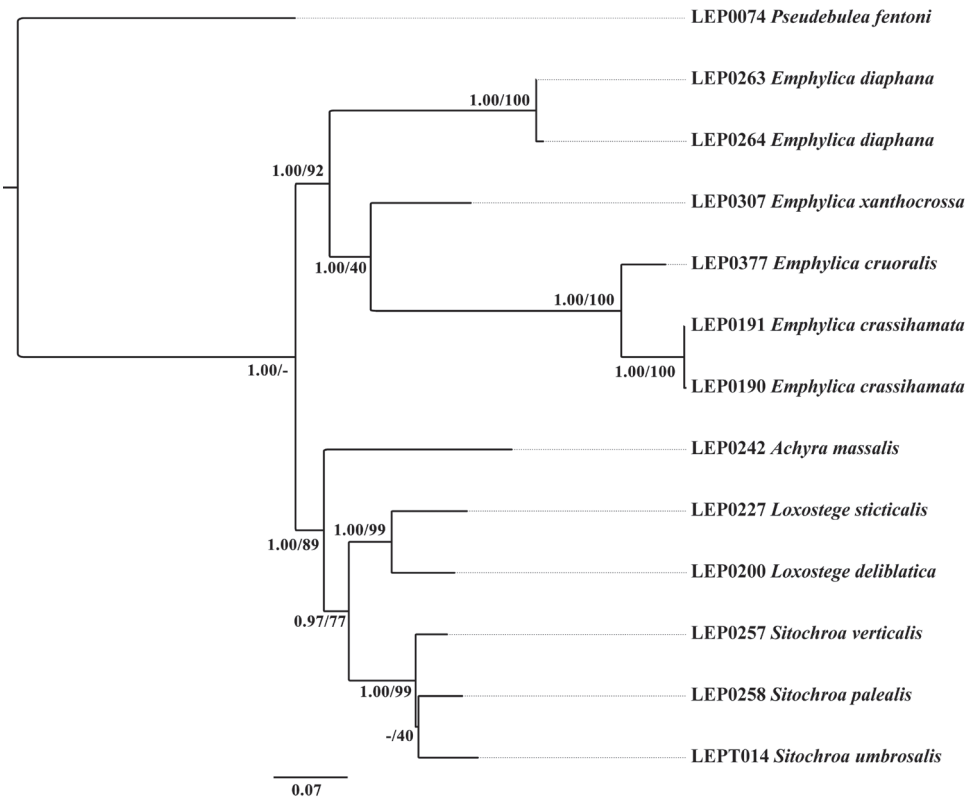


Figure 1. Phylogenetic hypothesis inferred from Maximum likelihood (ML) analysis. Numbers on branches indicate Bayesian posterior probabilities and ML bootstrap values, respectively.

Table 2. Pairwise distances of the COI barcode region based on Kimura-2-parameter model (intraspecific distances are highlighted in bold).

		1	2	3	4	5	6	7	8	9	10	11	12
1	LEP0190 *Emphylica crassihamata*												
2	LEP0191 *Emphylica crassihamata*	**0.000**											
3	LEP0263 *Emphylica diaphana*	0.083	0.083										
4	LEP0264 *Emphylica diaphana*	0.079	0.079	**0.008**									
5	LEP0307 *Emphylica xanthocrossa*	0.066	0.066	0.081	0.075								
6	LEP0377 *Emphylica cruoralis*	0.040	0.040	0.077	0.074	0.063							
7	LEP0200 *Loxostege deliblatica*	0.108	0.108	0.112	0.112	0.086	0.096						
8	LEP0227 *Loxostege sticticalis*	0.102	0.102	0.087	0.085	0.083	0.090	0.076					
9	LEP0242 *Achyra massalis*	0.100	0.100	0.092	0.096	0.098	0.089	0.090	0.083				
10	LEP0257 *Sitochroa verticalis*	0.123	0.123	0.112	0.108	0.104	0.116	0.090	0.087	0.116			
11	LEP0258 *Sitochroa palealis*	0.092	0.092	0.106	0.102	0.085	0.094	0.073	0.086	0.090	0.058		
12	LEPT014 *Sitochroa umbrosalis*	0.123	0.123	0.129	0.122	0.118	0.120	0.089	0.102	0.112	0.060	0.056	
13	LEP0074 *Pseudebulea fentoni*	0.133	0.133	0.144	0.141	0.135	0.146	0.147	0.144	0.148	0.155	0.137	0.159

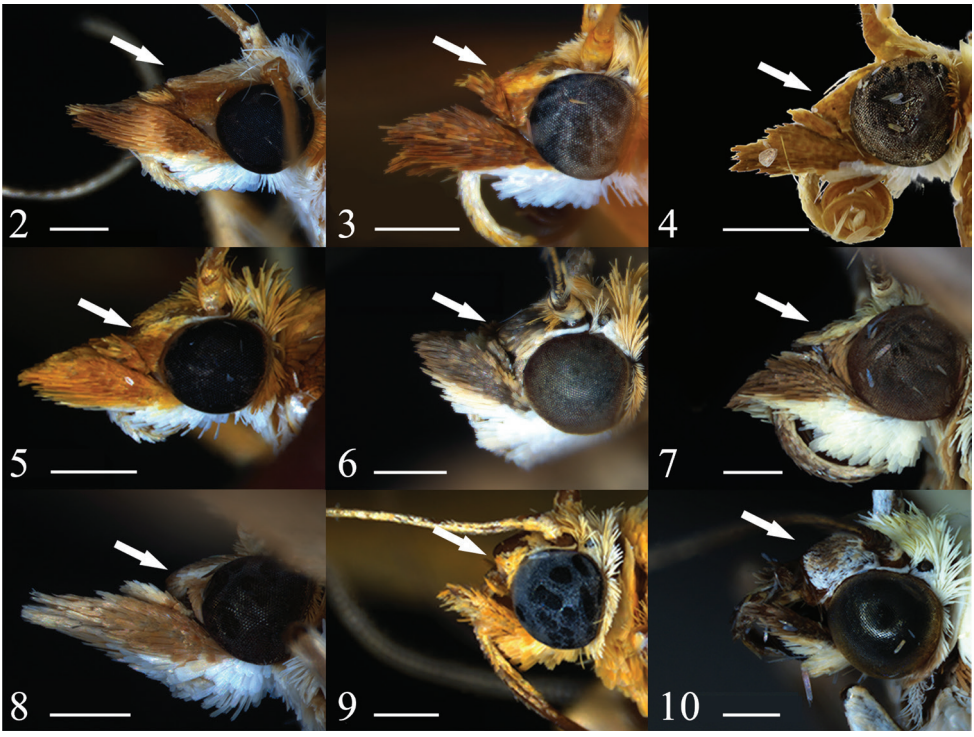
Taxonomy

Emphylica Turner, 1913

Emphylica Turner, 1913: 159. Type species: *Emphylica xanthocrossa* Turner, 1913, by monotypy.

Diagnosis. Species of *Emphylica* have a conical frons (Figs 2–5), similar to species of *Achyra*, *Loxostege* and *Sitochroa* (Figs 6–10), and by this differing from most genera of Pyraustinae. They can be best distinguished from the genera mentioned above in male genitalia by the narrowly triangular to trapezoid, sparsely to moderately setose uncus, the scale-liked editum, the sclerotized ventral process of the sella pointing towards the ventral margin of the valva, the nearly U-shaped juxta, the well-developed, distally rounded saccus, and the interlaced spicules in the phallus. In female genitalia, the antrum is sclerotized and the signum is rhombic.

Description. Head. Frons conical. Vertex with moderately raised scales projecting between antennae. Labial palpus slightly upwardly curved, approximately twice as long as diameter of eye; first segment with white scales at base; second segment obliquely directed upward; third segment long, porrect. Maxillary palpus prominent, curved upward. Proboscis well developed, with creamy white scales at base. Antenna in male with cilia shorter than or as long as width of corresponding flagellomeres. **Thorax.** Dorsal side whitish brown to brown; ventral side whitish to pale yellow. Legs unmodified, hindleg with basal inner spur longer than apical inner spur, approximately three times as long as basal outer spur. **Wings.** Forewing elongate-triangular, costa straight to near apex, then slightly arched to apex; apex sharp; termen weakly arched, oblique to tornus; dorsum straight; upperside usually with reddish or pale brown scales; frenulum hook in male well developed, retinaculum made up a tuft of curved bristles from below base of discal cell. Hindwing broad, fan-shaped; terminal margin usually brown; frenulum simple in male, with 2 acanthae in female. Wing venation as in Fig. 11. **Abdomen.** Apical margin of segments tinged with yellowish white. **Male genitalia.** Uncus narrowly triangular to narrowly trapezoid, more or less bulging near base. Tegumen trapezoid. Vinculum U-shaped. Saccus well developed, rounded triangular, approximately as long as uncus. Valva of medium width, tongue-shaped, slightly narrowed or tapering to rounded apex, ventral margin straight to slightly curved; transtilla short, triangular, usually with sclerotized ventral process extending to distal end of juxta; costal sclerotized band broad, slightly curved; dorsal sella short, lamellar, set with thick scale-like setae forming editum, more or less curved, apically with several filaments; ventral sella strongly sclerotized, usually perpendicularly pointing towards ventral margin of valva, usually curved apically; sacculus broad, usually with pointed sclerotized dorsal process (absent in *E. xanthocrossa*). Juxta usually U-shaped, distal arms sclerotized. Phallus tubular, usually with interlaced cornuti, in distal end with spine-like or teeth-like area of teeth. **Female genitalia.** Ovipositor lobes flat, densely setose. Posterior apophysis simple, anterior apophysis usually bulging near basal third.



Figures 2–10. Head profiles of species of *Emphylica*, *Loxostege*, *Achyra and Sitochroa* **2** *Emphylica diaphana* **3** *E. crassihamata* **4** *E. cruoralis* **5** *E. xanthocrossa*. **6** *Loxostege sticticalis* **7** *L. deliblatica* **8** *Achyra massalis* **9** *Sitochroa umbrosalis* **10** *S. palealis*. Scale bar: 0.5 mm.

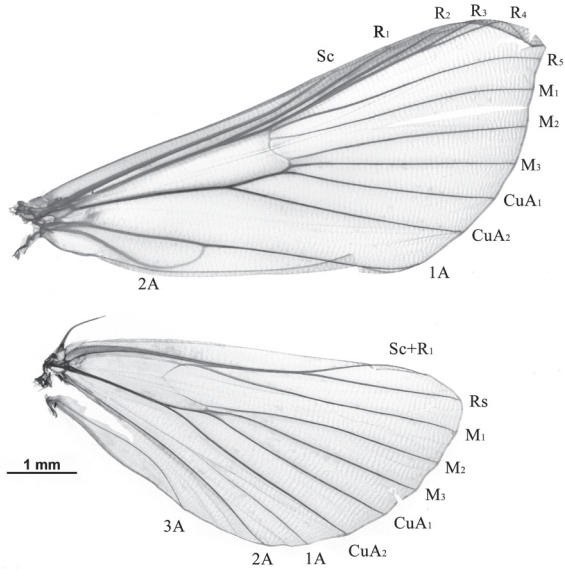


Figure 11. Wing venation of *Emphylica crassihamata*.

Antrum sclerotized. Ductus seminalis originating from anterior end of colliculum. Ductus bursae long and slender, more than 1.5× as long as diameter of corpus bursae. Corpus bursae globular, spinulose; accessory bursa present, arising from corpus bursae mediolaterally; signum narrowly rhombic to sea-star-shaped.

Biology. All of the Chinese material has been collected during the night at light. Host information is currently unavailable.

Distribution (Fig. 24). India, China, Australia.

Key to species of *Emphylica* based on males

1 Wingspan usually less than 15 mm (Fig. 15). Uncus concave distally, ductus ejaculatorius originating from the middle of the phallus (Fig. 19A, C) ..... ***E. xanthocrossa* Turner, 1913**

– Wingspan usually larger than 17 mm. Uncus not concave distally, ductus ejaculatorius originating from the anterior end of the phallus **2**

2 Ground colour of the wings whitish (Fig. 12). Uncus triangular, ventral sella reaching ventral margin of valva or beyond (Fig. 16A) ..... ***E. diaphana* (Caradja & Meyrick, 1934), comb. n.**

– Ground colour of the wings reddish brown or yellow. Uncus trapezoid, ventral sella not reaching ventral margin of valva (Figs 17A, 18A) **3**

3 Basal 2/3 of forewing predominantly reddish brown (Fig. 14). Ventral sella triangular, overlaid by a folded, distally blunt process (Fig. 18A, B) ..... ***E. cruoralis* (Warren, 1895), comb. n.**

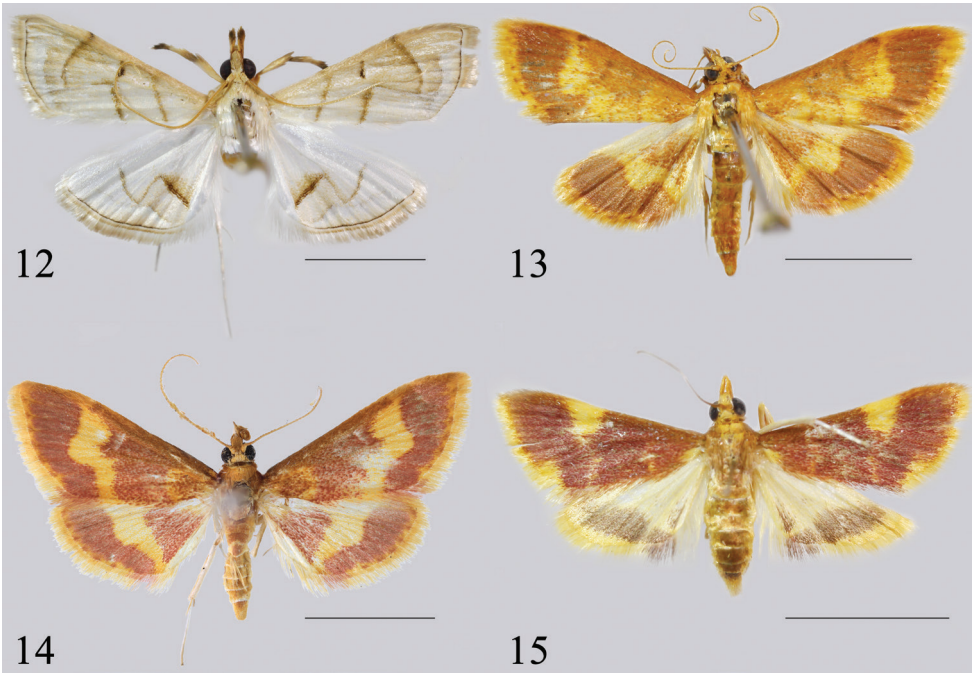
– Basal 2/3 of forewing yellow, sprinkled with reddish brown scales (Fig. 13). Ventral sella hook-like (Fig. 17A, B) ..... ***E. crassihamata* sp. n.**

***Emphylica diaphana* (Caradja & Meyrick, 1934), comb. n.**
Figs 2, 12, 16, 20, 24

Loxostege diaphana Caradja & Meyrick, 1934: 164.

Material examined. CHINA, Fujian: 1♂, Letu rain forest, Hexi, Nanjing, 24.90°N, 117.22°E, alt. 270 m, 10.VII.2014, leg. Zhang Dandan, genitalia slide no. SYSU1040, molecular voucher no. SYSU-LEP0263; **Guangdong:** 1♂, Sanyue Reserve, 24.03°N, 111.57°E, alt. 272 m, 6.VII.2013, leg. Chen Xiaohua, genitalia slide no. SYSU1041, molecular voucher no. SYSU-LEP0264; **Hainan:** 1♂, Mt. Limushan, 5.V.2011, leg. Zhang Dandan and Yang Lijun; **Chongqing:** 1♀, Daheba, Mt. Jinfoshan, alt. 800–850 m, 15.VII.2010, leg. Du Xicui and Song Lifang, genitalia slides no. SYSU0969; 1♂, Daheba, Mt. Jinfoshan, alt. 800–850 m, 16.VII.2010, leg. Du Xicui and Song Lifang, genitalia slides no. SYSU0965.

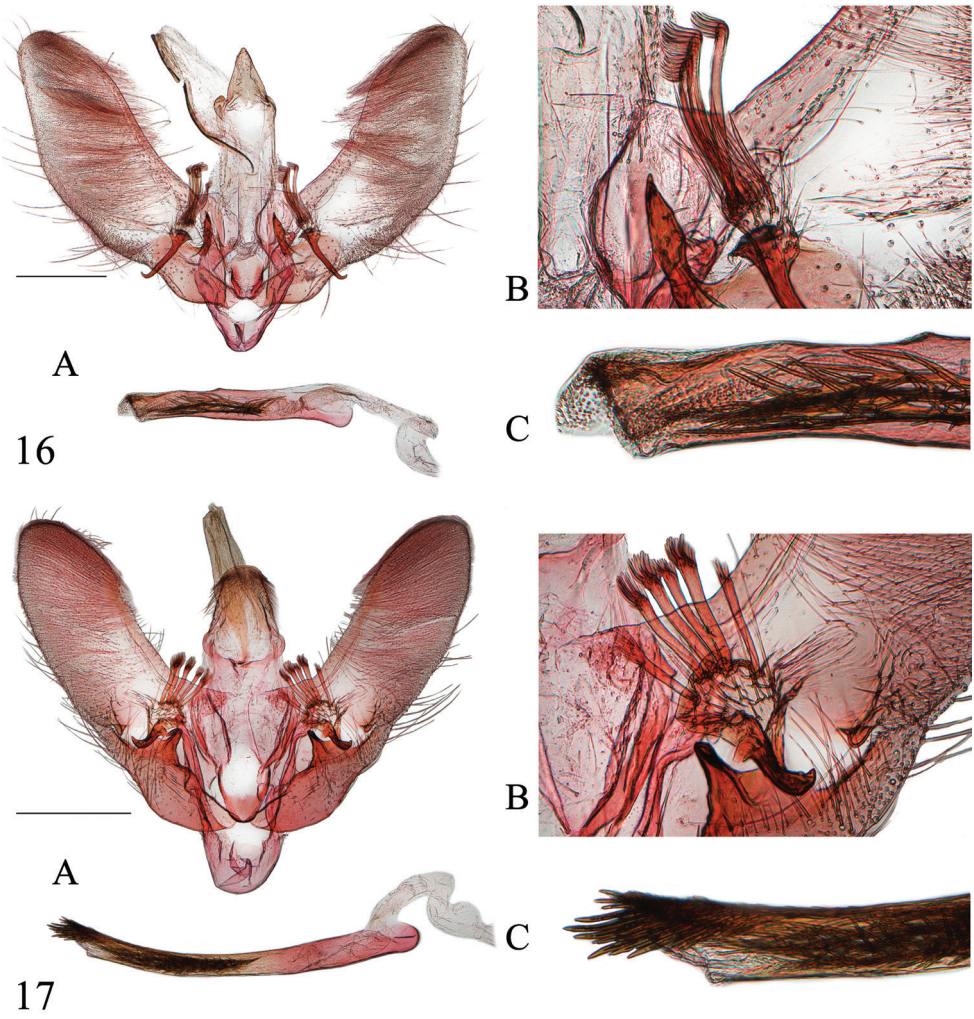
Diagnosis. *Emphylica diaphana* resembles other *Emphylica* species in the conical frons and the scale-like setae of the sella. It can be best distinguished from its con-



Figures 12–15. Adults of *Emphylica* spp. **12** *E. diaphana*, male (Hexi, Fujian) **13** *E. crassihamata*, holotype, male (Shixing, Guangdong) **14** *E. cruoralis*, male (Khasis, India) **15** *E. xanthocrossa*, female (Hidden Valley, Western Australia). Scale bar: 5.0 mm.

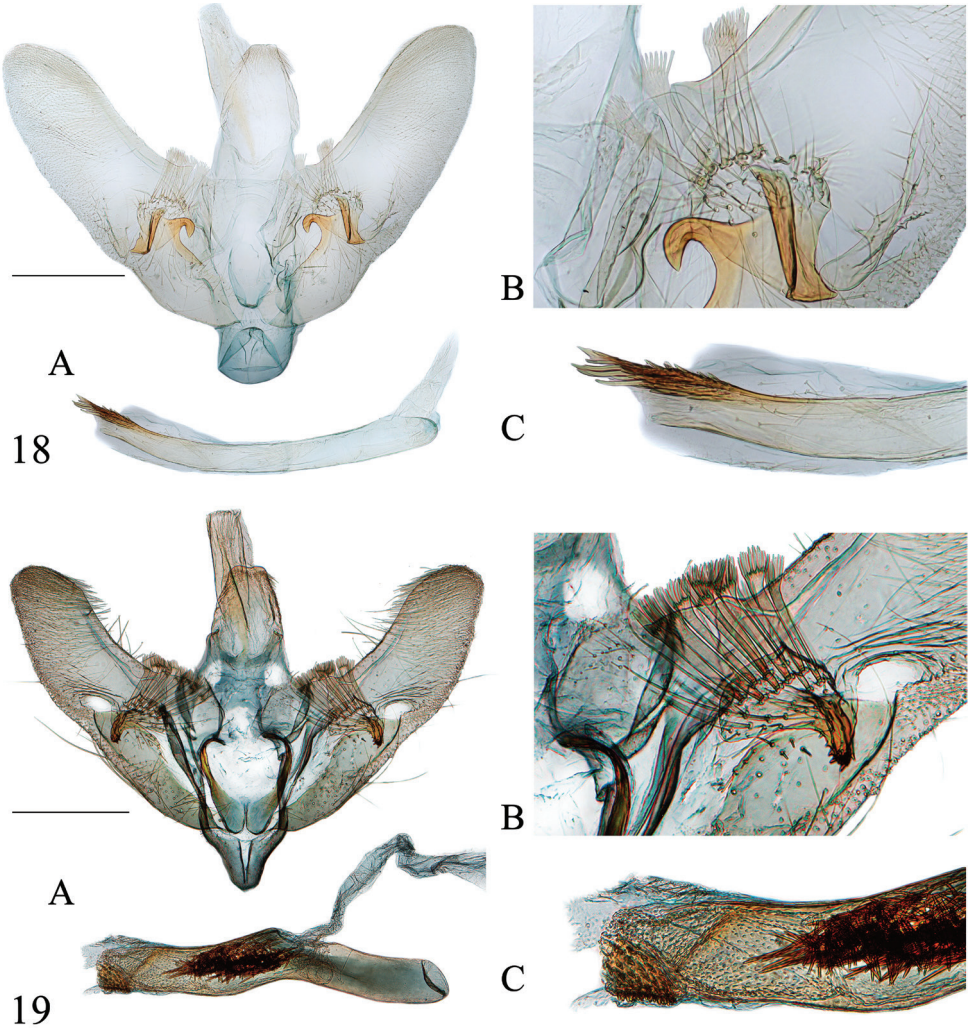
geners by the whitish ground colour suffused with pale brown scales on both wings, the dark brown lines at termen, in male genitalia by the triangular, distally narrowly-rounded uncus bearing only few short setae and the long, strongly sclerotized ventral sella usually projecting beyond the ventral margin of the valva. In female genitalia of *E. diaphana*, the antrum is strongly sclerotized, shorter than the length of the anterior apophysis, slightly wider than the ductus bursae; the maximal length of the signum is approximately 2/3 as long as the diameter of the corpus bursae; the two opposing angles of the signum without carinae are well-developed, almost as long as the other two. In *E. xanthocrossa* the antrum is broad, lightly sclerotized, no more than twice as wide as the ductus bursae; the two opposing angles of the signum without carinae are fairly short; in *E. crassihamata* the antrum is longer than the anterior apophysis, in *E. cruoralis* the antrum is as long as the anterior apophysis and the signum of both species is small (less than half of the diameter of the corpus bursae).

Redescription (Figs 2, 12). **Head.** Frons and vertex pale yellow mixed with few white scales. Antenna pale brown, cilia in male less than half as wide as corresponding flagellomeres. Labial palpus brown mixed with pale yellow medially, with white scales at base. Maxillary palpus brown, pale brown at tip. **Thorax.** Whitish brown at dorsum, whitish ventrally. Foreleg: femur yellow, ventrally white, tibia pale brown, first tarsus pale brown, second tarsus white mixed with pale brown, third and fourth tarsus dark brown, fifth tarsus white. Midleg: femur dorsally and tibia pale yellow, remainder whit-



Figures 16–17. Male genitalia of *Emphylica* spp. **16** *E. diaphana*, Chongqing (genitalia slide no. SYSU0965) **17** *E. crassihamata*, Guangdong (genitalia slide no. SYSU0933) **A** Whole genitalia **B** Base of valva dorsally **C** Distal part of phallus. Scale bar: 0.5 mm.

ish; inner spur about twice as long as outer one. Hindleg: pale yellow; basal inner spur approximately three times as long as basal outer spur; apical inner spur about twice as long as apical outer spur. Wingspan 17–19 mm. Forewing whitish sprinkled with pale brown. Antemedial line pale brown from basal third of costa, oblique, reaching beyond basal 1/4 of dorsum; reniform stigma a short streak, pale brown mixed with dark brown scales posteriorly; postmedial line brown, arched from beyond basal 2/3 of costa to about 2/3 of CuA_1, bent inwards to posterior angle of cell, then oblique to beyond half of dorsum; subterminal band whitish, with anterior 1/3 faint, gradually narrowed to tornus; termen line dark brown; fringe white at base and brown posteriorly. Hindwing white; postmedial line brown, darkened and thickened posteriorly,



Figures 18–19. Male genitalia of *Emphylica* spp. **18** *E. cruoralis*, Khasis (Pyralidae NHMUK Slide no. 10935) **19** *E. xanthocrossa*, Queensland (genitalia slide no. ANIC21185) **A** Whole genitalia **B** Base of valva dorsally **C** Distal part of phallus. Scale bar: 0.5 mm.

from base of Rs, weakly curved to about 2/3 of CuA_1, bent inwards to beyond base of CuA_1, then bent at right angle outwards to 3/4 of inner margin, latter section with pale brown anteriorly; subterminal line faint, from about 7/10 of M_2, weakly curved inwards to 3/4 of CuA_2, then slightly darkened, curved outwards to end of 2A; area between posterior part of posterior line and subterminal line sprinkled with few pale brown scales; terminal margin with few pale brown scales medially; termen edged by dark brown line; fringe as in forewing, entirely white near tornus. **Abdomen.** Dorsal segments pale brown, apical margins of basal four segments brown, edged by white scales, apical margins of remainder segments with white scales, 8th segment with two small dark brown spots posterolaterally; segments whitish ventrally. **Male genitalia**

(Fig. 16). Uncus narrow, triangular, bearing few hair-like setae at distal third. Valva with ventral margin curved, gradually narrowed towards obtusely rounded apex; costal sclerotized band wide, slightly curved to 2/3 of dorsal margin; sacculus broad, distal half expanded, with a pointed, strongly sclerotized process projecting dorsally, sparsely setose; dorsal sella sub-rectangular; ventral sella long and slender, strongly sclerotized, distally curved, usually reaching or extending beyond ventral margin of valva. Juxta plate-shaped with lateral part strongly sclerotized, distal half slightly divided medially. Phallus tubular, straight, approximately 4/5 as long as length of valva, distal half with interlaced spicules, distal end dorsally with several small, teeth-like spines. **Female genitalia** (Fig. 20). Anterior apophysis with triangular expansion near basal third. Antrum cup-shaped, slightly wider than ductus bursae, medially somewhat constricted. Ductus bursae slender, approximately 2× as long as diameter of corpus bursae; colliculum well developed, slightly sinuate laterally, approximately as long as antrum. Corpus bursae globular; accessory bursa globular; signum sea-star-shaped, with two angles bearing carinae disconnected medially, distally pointed, other two angles well developed, distally rounded.

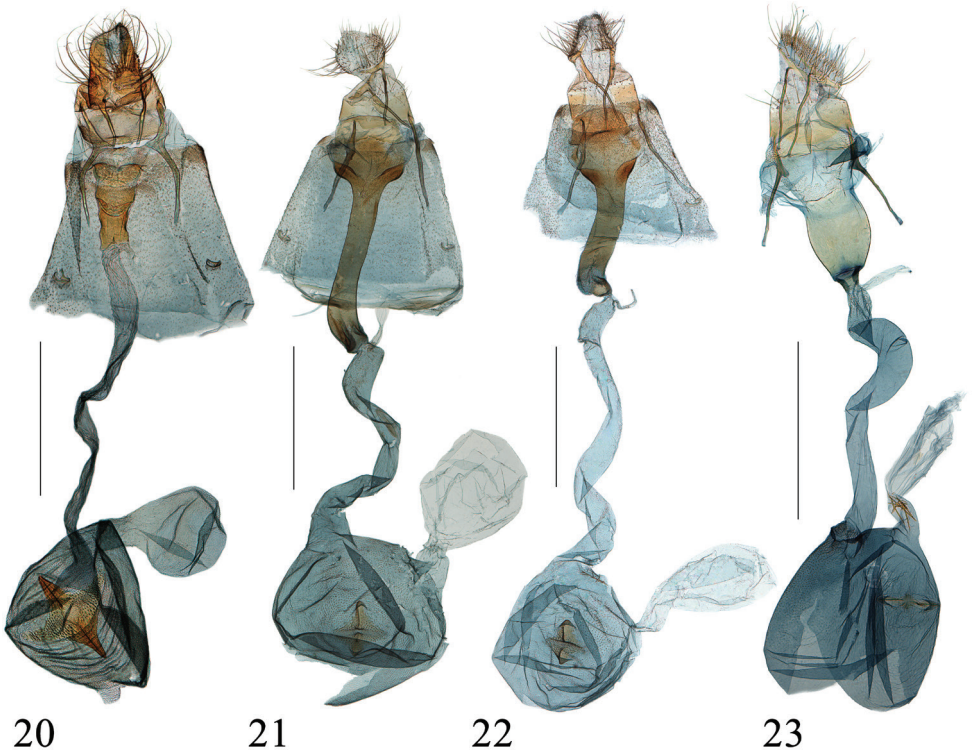
Distribution (Fig. 24). China (Fujian, Guangdong, Hainan, Chongqing).

Remarks. This species was formerly placed in the genus *Loxostege*, probably based on the conical frons. However, genitalia traits of *Loxostege* moths, e.g. the cylindrical uncus with dense, scale-like setae, the few hair-like setae of the dorsal sella, the ventrobasally directed ventral sella and the usually coiled ductus bursae, are different in *Emphylica diaphana*. Although in appearance the wing colour and pattern of this species are somewhat dissimilar to those of other *Emphylica* species, the genitalia traits agree with the diagnostic characters of *Emphylica xanthocrossa* Turner, the type species. Moreover, according to the molecular phylogeny, this species was inferred as terminal lineage within *Emphylica*, rather than in *Loxostege*. Consequently, this species is considered as correctly placed in *Emphylica*.

Emphylica crassihamata Chen & Zhang, sp. n.

http://zoobank.org/F348D37E-4CA9-41A5-89CE-09866C0B0B4F
Figs 3, 11, 13, 17, 21, 24

Material examined. Type material. Holotype ♂ (Fig. 13); **CHINA, Guangdong:** Chebaling National Nature Reserve, Shixing County, 24.72°N, 114.26°E, alt. 496 m, 28.V.2017, leg. Chen Kai. Paratypes: **Hunan:** 1♂, Mt. Huilongshan, Zixing, 26.08°N, 113.39°E, alt. 886 m, 8.VI.2016, leg. Chen Kai and Duan Yongjiang; 1♂, Jinyinpu, Bamianshan Reserve, Guidong County, 25.97°N, 113.71°E, alt. 973 m, 16.VI.2015, leg. Chen Kai; 2♀, Gaowangjie National Nature Reserve, Guzhang County, 28.66°N, 110.08°E, alt. 890 m, 18.VI.2017, leg. Zhang Dandan, genitalia slides no. SYSU0994 (molecular voucher no. SYSU-LEP0191), 0957; **Guangdong:** 1♂, same data as holotype; 2♂, idem except leg. Duan Yongjiang, genitalia slide no. SYSU0993, molecular voucher no. SYSU-LEP0190; 2♂, idem except leg. Kou Zongqing, genitalia slide no. SYSU0933.



Figures 20–23. Female genitalia of *Emphylica* spp., ventral views **20** *E. diaphana*, Chongqing (genitalia slide no. SYSU0969) **21** *E. crassihamata*, Hunan (genitalia slide no. SYSU0957) **22** *E. cruoralis*, Tibet (genitalia slide no. ZDD12100) **23** *E. xanthocrossa*, Queensland (genitalia slide no. ANIC18162). Scale bar: 1.0 mm.

Diagnosis. In appearance, *E. crassihamata* resembles *E. cruoralis* in the reddish brown subterminal band, but can still be recognized by the predominantly yellow basal 2/3 of the forewing sprinkled with reddish brown scales and the presence of a faint antemedial line on the forewing and postmedial lines on both wings. In male genitalia it differs from *E. diaphana* and *E. xanthocrossa* by the distally rounded, moderately setose uncus, the pointed and recurved dorsal process of the sacculus, and the long and slender phallus, which is longer than the length of the valva; from *E. cruoralis* it differs by the wider distal uncus, the small triangular, strongly sclerotized process near the distal sacculus as well as the hook-like ventral sella. In female genitalia, the sclerotized antrum is approximately 1.5× as long as the anterior apophysis whereas in *E. cruoralis* the sclerotized antrum is as long as the anterior apophysis.

Description (Figs 3, 13). **Head.** Frons and vertex yellowish brown, frons with cream white stripe laterally. Antenna yellowish brown, cilia in male as long as width of corresponding flagellomeres. Labial palpus brown with white scales at base. Maxillary palpus brown. **Thorax.** Saffron dorsally, pale yellow ventrally. Foreleg: femur brown; tibia brown and white alternately; tarsi white except distal three brown. Midleg: femur

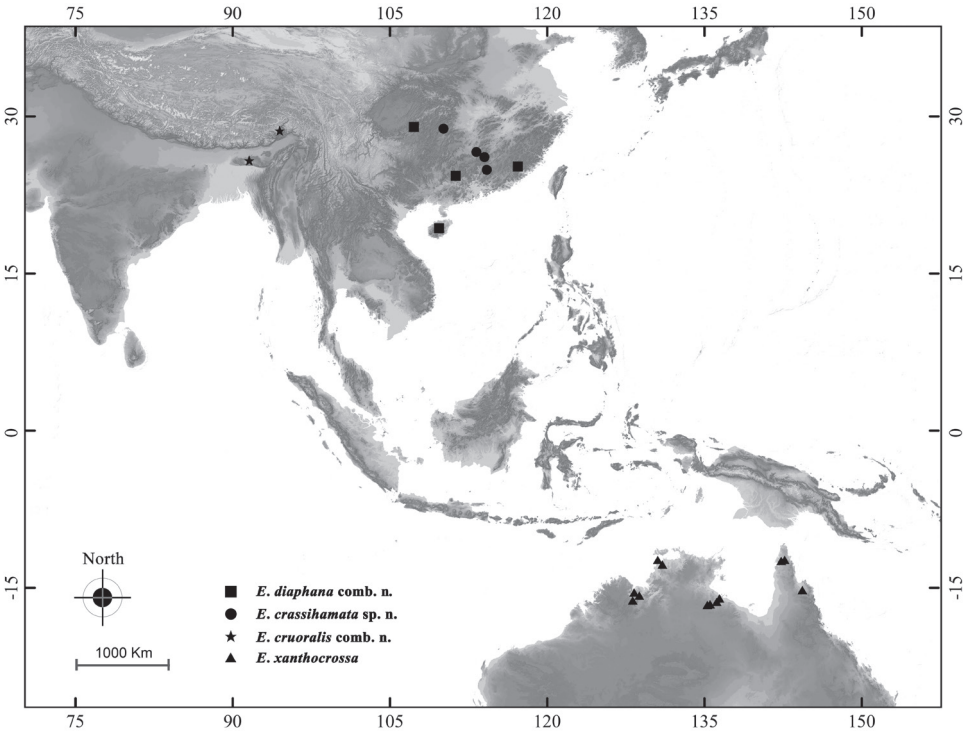


Figure 24. Distribution map of *Emphylica* spp.

pale brown; tibia yellow dorsally, white ventrally, outer spur half as long as inner one; tarsi white ventrally, pale yellow dorsally. Hindleg: femur pale brown; tibia yellow, basal inner spur in male about three times as long as basal outer spur, apical inner spur about twice as long as apical outer spur; tarsi pale yellow. Wingspan 17.5–18.5 mm. Forewing yellow edged by reddish brown subterminal band, sprinkled with reddish brown scales from base to postmedial line, slightly darkened along costal margin, veins covered with reddish brown scales terminally, terminal band narrow, saffron; antemedial line reddish brown, curved outwards from basal fourth of costa to about basal third of dorsum; orbicular stigma faint, dark brown; reniform stigma straight, strip-like, dark brown; postmedial line reddish brown, weakly sinuate from 3/4 of costa to base of M_2, bent inwards to base of CuA_2, then curved outwards to about middle of dorsum; inner margin of subterminal band nearly parallel to postmedial line; underside with ground colour as on upperside but paler; fringe saffron mixed with pale yellow scales, mostly reddish brown at tornus. Hindwing with costal margin translucent white to 2/3 of costa, basal half medially pale reddish brown, followed by pale yellow band, outer margin sinuate, edged by reddish brown subterminal band, terminal band narrow, saffron, veins with reddish brown scales terminally; postmedial line indistinct; fringe as in forewing; underside paler than upperside especially in basal half. **Abdomen.** Brown dorsally, whitish ventrally, apical margins of segments tinged with white.

Male genitalia (Fig. 17). Uncus bulging at base, gradually narrowed towards obtusely rounded apex, maximal width approximately 2× minimal width, bearing hair-like setae on distal half. Valva evenly wide medially, slightly tapering towards apex, with a small triangular sclerotized process beyond distal end of sacculus; transtilla triangular; costal sclerotized band wide, slightly expanded to 2/3 of dorsal margin; sacculus broad, distal third expanded and bearing a strongly sclerotized, hook-like process; dorsal sella quadrate; ventral sella hook-like, strongly sclerotized. Juxta U-shaped with two slender arms, thickened and fused in basal half. Phallus long and slender, slightly curved upward, approximately 1.25× length of valva, distal half with interlaced spicules on vesica, distal end with several pointed cornuti dorsally. **Female genitalia** (Fig. 21). Anterior apophysis slightly bulging near basal third. Antrum long, funnel-shaped, thickened and strongly sclerotized distolaterally, approximately 1.5× as long as anterior apophysis. Ductus bursae slender, as wide as anterior part of antrum, approximately 1.8× as long as diameter of corpus bursae; colliculum slightly narrowed posteriorly. Corpus bursae globular, spinulose; accessory bursa arising from middle side of corpus bursae; rhombic signum small, maximal length approximately 1/3 as long as diameter of corpus bursae, with two opposing angles bearing carinae disconnected medially, other two angles triangular, distally blunt.

Etymology. The specific name is derived from the Latin *crassi-* = thick and *hamata* = hook-like, referring to the thick, hook-like ventral sella.

Distribution (Fig. 24). China (Hunan, Guangdong).

Emphylica cruoralis (Warren, 1895), comb. n.
Figs 4, 14, 18, 22, 24

Syllythria cruoralis Warren, 1895: 471.
Pyrausta cruoralis (Warren, 1895): Hampson 1896: 432.

Material examined. Type material. Lectotype (here designated) ♂: **INDIA, Meghalaya:** Khasis, Mar.1894, Nat. Coll., Pyralidae NHMUK Slide no. 10935 (NHMUK).

Other material examined. INDIA, Meghalaya: 7♂ (Fig. 14), Khasia Hills, Assam, Nissary (NHMUK); 8♂, Assam, Khasis, Nat. Coll. (NHMUK); 1♂, same data as type (NHMUK); 1♂, Khasis Hills, Assam (NHMUK); 1♂, Khasis Hills (NHMUK); **CHINA, Tibet:** 1♀, air-raid shelter, Beibeng Village, Medog County, 29.24°N, 95.17°E, alt. 750 m, 31.VII.2018, leg. Qi Mujie, genitalia slide no. ZDD12100 (molecular voucher no. SYSU-LEP0377) (NKU).

Diagnosis. *Emphylica cruoralis* resembles *E. crassihamata* in the reddish brown subterminal band and the saffron fringe. The differences between the two species are provided in the diagnosis of *E. crassihamata*. In appearance, *E. cruoralis* can be best recognized within the genus by the yellow postmedial band of the forewing, in male genitalia by the narrow trapezoid uncus with hair-like setae at distal third, the large, thumb-shaped, weakly sclerotized process of the ventral valva near the distal sacculus as

well as the triangular ventral sella overlaid by a folded, distally blunt process. In female genitalia, it resembles *E. crassihamata* except for the less sinuate distolateral antrum and the relatively shorter and wider antrum anteriorly.

Redescription (Figs 4, 14). **Head.** Frons and vertex yellowish brown. Antenna pale yellowish brown, cilia in male as long as width of corresponding flagellomeres. Labial palpus yellowish brown with white scales at base. Maxillary palpus yellowish brown. **Thorax.** Yellowish brown dorsally, whitish ventrally. Foreleg: femur brown; tibia brown and white alternately; tarsi white except for pale brown distal three. Midleg: femur pale brown; tibia yellow on dorsum, white ventrally, outer spur half as long as inner one; tarsi white ventrally, pale yellow dorsally. Hindleg: yellowish brown, basal inner spur in male about three times as long as basal outer spur, apical inner spur about twice as long as apical outer spur. Wingspan 16–19 mm. Forewing with reddish brown ground colour, except for saffron circle at base and sinuate, saffron postmedial band, narrowing towards costa and dorsum; costa straight, slightly arched to apex, brown at basal 2/3, yellowish brown at distal third; terminal margin with narrow, saffron intermittent band; fringe saffron, mixed with reddish brown near tornus. Hindwing with costal margin translucent white to 2/3 of costa, basal half medially reddish brown, followed by yellow postmedial band, narrowing towards tornus, outer margin sinuate, edged by reddish brown subterminal band, terminal band narrow, intermittent, saffron, posterior margin pale yellow; fringe as in forewing. **Abdomen.** Dorsally yellowish brown, apical margins of segments tinged with white. **Male genitalia** (Fig. 18). Uncus slightly bulging at base, gradually narrowed towards truncate apex, maximal width approximately 3× minimal width, distal third with hair-like setae. Valva evenly wide medially, slightly tapering towards rounded apex, ventral margin with weakly sclerotized, thumb-shaped process projecting basally near distal end of sacculus; costal sclerotized band moderately wide, slightly curved to beyond 2/3 of dorsal margin; sacculus broad, distal third expanded and bearing a strongly sclerotized, hook-like process; ventral sella triangular, weakly sclerotized, overlaid by strongly sclerotized, folded, distally blunt process. Juxta U-shaped with two narrow tapering arms, basally broadened. Phallus as in *E. crassihamata* (without interlaced spicules of vesica in Fig. 18). **Female genitalia** (Fig. 22). As in *E. crassihamata* except: distolateral antrum less sinuate, relatively shorter and wider anteriorly; ductus bursae narrower than width of anterior part of antrum.

Distribution (Fig. 24). India (Meghalaya), China (Tibet).

Remarks. This species was formerly placed in the genus *Pyrausta*. However, both the molecular phylogeny and the genital traits suggested that it should be placed in *Emphylica*. According to the male genitalia (Fig. 18) of the type specimen of *Emphylica cruoralis* (Warren, 1895), **comb. n.**, this species agrees with diagnostic characters of *Emphylica*. It differs from *Pyrausta* by the conical frons, in male genitalia by the the presence of an editum made of modified, scale-like setae, the more anteriorly positioned and ventrally directed and sclerotized sella, and the more strongly developed sclerotized dorsal process of the sacculus, and in female genitalia (Fig. 22) by the strongly sclerotized antrum.

***Emphylica xanthocrossa* Turner, 1913**
Figs 5, 15, 19, 23, 24

Emphylica xanthocrossa Turner, 1913: 159.

Material examined. Type material. Holotype, ♀: **AUSTRALIA, Northern Territory:** P[ort]. Darwin, Nov.[19]08, leg. F.P. Dodd, genitalia slide no. P232 (ANIC).

Other material examined (ANIC). **AUSTRALIA, Northern Territory:** 1♂, 16.19°S, 136.05°E, 36 km SW of Borroloola, NT, 4.Nov.1975, leg. E.D. Edwards, K. Maes Gen. Prep. nr.: 20741; genitalia slide no. ANIC18161; 1♂, 16.10°S, 136.15°E, Goose Lagoon, 11 km SW by S Borroloola, NT, 31.Oct.1975, E.D. Edwards leg.; 1♂, Humpty Doo, N.T., Light Trap, 10.Nov.1959, E.B. Boerema leg.; 2♂, 16.40°S, 135.51°E, Bessie Spring, 8 km ESE of Cape Crawford, NT, 26.Otc.1975, E.D. Edwards leg., genitalia slide no. P707; 1♀, 16.41°S, 135.44°E, Cape Crawford road junction, NT, 29.Mar.1995, E.D. Edwards and M. Matthews leg.; **Queensland:** 1♂, 15.45°S, 144.15°E, 2 km NNW of Jowabinna, 17.I.1994, E.D. Edwards and P. Zborowski leg., genitalia slide no. ANIC21185; 1♀, 12.42°S, 142.30°E, Moonlight creek, QLD, 13.Nov.1993, at light, P. Zborowski and M. Horak leg., K. Maes Gen. Prep. nr.: 20742, genitalia slide no. ANIC18162; 1♂, 12.40°S, 142.40°E, Batavia Downs, QLD, 22-23.Nov.1992, at light, P. Zborowski and A. Calder leg.; 1♂, 12.40°S, 142.41°E, Batavia Downs, QLD, 11.Dec.1992, at light, P. Zborowski and W. Dressler leg.; **Western Australia**: 1♀, 15.77°S, 128.75°E, Hidden Valley, Kununurra, III.2016, P.M. Heath leg., genitalia slide no. ANIC21184, molecular voucher no. SYSU-LEP0307; 1♂, Kunnunurra, W.A., 9.Apr.1962, I.F.B. Common leg.; 1♂, Wyndham, W.A., ?.?.[19]30, T.G. Campbell leg.; 1♂, 16.10°S, 128.23°E, nr Dunham River crossing, WA, 6.Apr.1995, E.D. Edwards and M. Matthews leg.

Diagnosis. *Emphylica xanthocrossa* resembles *E. crassihamata* and *E. cruoralis* in the saffron fringe, the conical frons and the U-shaped juxta. It can be best distinguished from its congeners by the smaller wingspan (less than 15 mm), the triangular saffron spot on the forewing costa postmedially, the smoky brown subterminal margin of the hindwing, in male genitalia by the distally concave uncus, the spinulose ventral sella, the absence of a dorsal process on the sacculus, the larger juxta, the broad and slightly sinuate phallus and the ductus ejaculatorius originating from the middle of the phallus. In female genitalia, the antrum is moderately sclerotized, bottle-shaped, the two opposing angles of the signum without carinae are short, whereas in *E. diaphana*, *E. crassihamata* and *E. cruoralis* the antrum is strongly sclerotized and the two opposing angles of the signum without carinae are almost as long as the other two.

Redescription (Figs 5, 15). **Head.** Frons and vertex pale yellowish brown, frons with cream white stripe laterally. Antenna brown, cilia in male less than half width of corresponding flagellomeres. Labial palpus brown and pale yellow alternately with white scales at base, pale yellow at tip. Maxillary palpus yellowish brown. **Thorax.** Pale yellow dorsally, whitish ventrally. Foreleg: yellow except distally white tibia and

alternately yellow and white tarsi. Midleg: pale yellow, tibia and tarsi white ventrally; inner spur about twice as long as the outer one. Hindleg: yellowish white; basal outer spur reduced; apical inner spur about 3× as long as apical outer spur. Wingspan 13–14 mm. Forewing reddish brown, with a large triangular to sub-quadrate saffron spot on costa postmedially, a small saffron spot at base of dorsum and a semi-oval saffron patch at termen near tornus; antemedial and postmedial lines almost invisible except near dorsum; costal margin pale brown except at yellow spot; terminal margin mixed with saffron; fringe saffron; underside as upper side but paler, translucent at dorsum. Hindwing with costal margin translucent white to 2/3 of costa; termen arched to 1/2 then strongly oblique to tornus; distal third smoky brown except for saffron terminal area from apex to 1A; below posterior angle of cell covered with few brown scales, and a triangular patch of brown scales near tornus; remainder pale yellow; fringe as in forewing except brown near tornus; underside pale yellow. **Abdomen.** Dorsally covered with saffron scales, whitish ventrally, apical margin of segments tinged with yellowish white. **Male genitalia** (Fig. 19). Uncus with lateral margin slightly bulging at base, then gradually narrowed to concave apex, setose on distal third. Valva evenly wide in middle, tapering to rounded apex; transtilla triangular; costal sclerotized band wide, slightly curved to 2/3 of dorsal margin; sacculus broad, distal half moderately expanded; dorsal sella sub-rectangular; ventral sella triangular, slightly flexed and curved, spinulose, distally blunt. Juxta large U-shaped with two strongly sclerotized, curved, tapering distal arms, thickened basally and medially divided. Phallus tubular, slightly sinuate, approximately 1.1× length of valva, distal fourth spinulose, apically with dense, teeth-like spines ventrally; ductus ejaculatorius originating from middle of phallus; vesica with bundle of interlaced spicules. **Female genitalia** (Fig. 23). Posterior apophysis long and slender, approximately 4/5 as long as anterior apophysis. Anterior apophysis with triangular expansion near basal third. Antrum moderately sclerotized, bottle-shaped, slightly bulging medially. Ductus bursae slender, approximately 1.4× as long as diameter of corpus bursae; colliculum slightly narrowed medially. Corpus bursae globular; rhombic signum small, maximal length approximately 1/3 as long as diameter of corpus bursae, with two distally pointed opposing angles bearing carina disconnected medially, other two angles small, indistinct.

Distribution (Fig. 24). Australia (Northern Territory, Queensland, Western Australia).

Discussion

Based on the molecular phylogeny, the clade *Achyra* + (*Loxostege* + *Sitochroa*) is a sister group to *Emphylica*. All these four genera have a similar conical frons. Species of *Achyra* can be distinguished from *Emphylica* in male genitalia by the narrow triangular uncus laterally set with dense hair-like setae, the dense simple setae of the sella and in female genitalia by the presence of a second signum and the broad base of the ductus seminalis. Species of *Loxostege* differ from *Emphylica* in male genitalia by the cylindrical uncus set with scale-like setae, the few simple setae of the sella and in female genitalia by the long

and coiled ductus bursae with a sclerotized base. Species of *Sitochroa* are best distinguished from *Emphylica* in male genitalia by the ventral sella with two hook-like, basally curved processes and the strongly sclerotized process extending from the phallus apically, and in female genitalia by the twisted sclerite near the posterior end of the ductus bursae. *Hahncappsia*, *Neohelvibotys* and *Helvibotys*, mainly distributed in the Nearctic and Neotropical regions, are not included in the current phylogenetic analysis. External characters of these three genera are similar to those of *Achyra*, *Loxostege* and *Sitochroa* (Munroe, 1976a). The morphological details were provided by Munroe (1976a, b). In male genitalia, *Emphylica* moths can be best distinguished from species of *Hahncappsia*, *Neohelvibotys* and *Helvibotys* by the usually trapezoid uncus, the thick, scale-like editum and the well-developed, distally rounded saccus. Some species of *Hahncappsia* have a row of scale-like setae on the sella and the sclerotized process of the sacculus is similar to those of *Emphylica*. The relationships between all these genera need to be further studied.

The monophyly of *Emphylica* is robustly supported by the results of the molecular analysis. Four species can be recognized as members of *Emphylica* based on the series of morphological characters provided above in the diagnosis of the genus. According to the tree topology (Fig. 1), *E. crassihamata* + *E. cruoralis* and *E. xanthocrossa* form a separate group, but with relatively low support in the ML analysis (BS = 40). Both BI and ML analyses show the same topologies, suggesting that *E. crassihamata* and *E. cruoralis* are more closely related to *E. xanthocrossa* than to *E. diaphana* which makes good sense with respect to the wing colouration. Within the genus, *E. crassihamata* is most closely related to *E. cruoralis* in the hindwing pattern (Figs 13, 14) and the genitalia (Figs 17, 18, Figs 21, 22).

Emphylica is recorded for the first time from outside Australia. The current study shows that *Emphylica* species occur in Southern China, the northwest of India and the north of Australia. There is as yet no record of *Emphylica* species in Indochina and the Malay Archipelago. Noteworthily, there are three *Pyrausta* spp., probably congeneric with *Emphylica*, recorded in Borneo (see http://www.pyralidsofborneo.org/index.php?cruoralis; http://www.pyralidsofborneo.org/index.php?sp4-17; http://www.pyralidsofborneo.org/index.php?sp5-10). The specimen identified as *P. cruoralis* is very similar to *E. cruoralis* in wing pattern, but with much narrower yellow bands on both wings. The wing pattern of another specimen identified as *P.* sp4 is almost the same as the former specimen, but the wingspan is similar to that of *E. xanthocrossa*. The last specimen identified as *P.* sp5 also has yellow bands of both wings similar to those of *E. cruoralis*. Unfortunately, the frons of these specimens cannot be observed, and no image of genitalia or genetic data can be accessed. Considering the similarity in the wing pattern, it would not be a surprise if these three taxa turn out to be congeneric with *Emphylica* species.

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DATA PAPER

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Batumi Raptor Count: autumn raptor migration count data from the Batumi bottleneck, Republic of Georgia

Jasper Wehrmann[1], Folkert de Boer[1,2], Rafa Benjumea[1], Simon Cavaillès[1], Dries Engelen[1], Johannes Jansen[1], Brecht Verhelst[3], Wouter M.G. Vansteelant[1,4]

1 *BRC Foundation, Dijkgraaf 35, 6721NJ Bennekom, The Netherlands* **2** *Zostera B.V., Halve Raak 30, 2771 AD Boskoop, The Netherlands* **3** *BirdLife Europe and Central Asia, Avenue de la Toison d'Or 67 (2nd floor), 1060 Brussels, Belgium* **4** *Computational and Theoretical Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, The Netherlands*

Corresponding author: *Jasper Wehrmann* (jasper.wehrmann@batumiraptorcount.org)

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Abstract

One of the most important geographical bottlenecks for migrating raptors in the east African-Palearctic migration system is situated between the easternmost tip of the Black Sea and the Lesser Caucasus, just north of Batumi, in the Republic of Georgia. Since 2008, citizen scientists of the Batumi Raptor Count (BRC) have monitored the autumn raptor passage daily from mid-August until mid-October, collecting also detailed information about the age and sex of focal species. The full BRC dataset was recently made available through the Global Biodiversity Information Facility (GBIF). Here we describe how count data were collected, managed, and processed for trend analysis over the past 10 years. This dataset offers a unique baseline for monitoring the state of migrant raptor populations in the east African-Palearctic flyway in the 21st century. We discuss potential pitfalls for users and hope that the open access publication of our data will stimulate flyway-scale and continent-wide collaboration for raptor migration monitoring in the Old World.

Keywords

Black Sea flyway, birds of prey, bottleneck, citizen science

Introduction

Counting migrant birds at strategic geographical locations, such as coastlines and topographic leading lines, may be a cost-effective way of monitoring trends in the abundance of wide-ranging common species and the timing of their migration. Migration counts can even offer an alternative to breeding bird surveys for species that behave secretively or breed in remote parts of the world or inaccessible habitats. Thus, monitoring sites across the globe along major flyways for soaring birds were established in the 20th century, and standardized migration counts have been used ever since to monitor migrant raptors across the globe (Bednarz et al. 1990; Kjellen and Roos 2000; Shirihai et al. 2000; McCarty and Bildstein 2005; Bensusan et al. 2007; Farmer et al. 2007; Filippi-Codaccioni et al. 2010; Martín et al. 2016). At the beginning of the 21st century, new monitoring sites were established in important raptor migration flyways, such as those in Costa Rica and Panama along the Central American flyway (Porras-Peñaranda et al. 2004; Batista et al. 2005), Radar Hill and Khao Dinsor in Thailand (DeCandido et al. 2004, 2008), and Thoolakharka in Nepal (DeCandido 2013). In this paper, we describe raptor migration count data collected by the Batumi Raptor Count (BRC), a raptor migration count project which was established in 2008 along the eastern Black Sea coast in the Republic of Georgia.

Various naturalists have reported on the mass aggregation of migrant raptors along the eastern Black Sea flyway (Villkonskii 1897; Andrews et al. 1977; Magnin 1989; Van Maanen et al. 2001; Abuladze 2008, 2013). With this in mind, the BRC project mobilized an international team to conduct a two-month survey in the area in 2008 and 2009. This team included several dozen volunteers, of which most were experienced migration counters and bird watchers. These pilot counts revealed that the numbers of raptors converging in the Batumi bottleneck were much larger than previously estimated, making the eastern Black Sea flyway one of the most important flyways in the African-Palearctic migration system and including over 1% of the global population of 10 raptor species (Verhelst et al. 2011). It hosts, by far, the most concentrated autumn passage of European Honey-buzzard *Pernis apivorus* (Linnaeus, 1758), Montagu's Harrier *Circus pygargus* (Linnaeus, 1758), Pallid Harrier *Circus macrourus* (Gmelin, 1770), and Western Marsh-harrier *Circus aeruginosus* (Linnaeus, 1758) recorded anywhere in the world.

By 2011, BRC settled on a count protocol targeting those species for which migration counts are most likely to capture ecologically relevant population trends and, thus, likely to provide a useful monitoring instrument, which can be used for conservation purposes. Target species were selected based on (1) the relevance of the annual flight at Batumi relative to global population estimates (Verhelst et al. 2011), (2) species' conservation status, and (3) species-specific flight behavior and timing, e.g. the ease with which species can be counted. For example, soaring migrants are relatively easy to count as they often pass in large streams, usually clearly visible from a vantage point and within a few 100 meters above the landscape. In contrast, many small raptors (e.g. Eurasian

Sparrowhawk *Accipiter nisus* Linnaeus, 1758) are difficult to count as they pass solitarily and low above ground and the forest canopy, especially under cloudy conditions.

Targeting specific species allows us to better standardize our count effort and to obtain better data quality. That is, we are able to record higher proportions of observations with accurate identification, age, sex, and other relevant information. Furthermore, we fine-tuned our count strategies between species to obtain the highest possible quality of count data under local conditions. In addition to raptors, we also decided to record European Roller *Coracias garrulus* (Linnaeus, 1758), European Turtle-dove *Streptopelia turtur* (Linnaeus, 1758), White Stork *Ciconia ciconia* (Linnaeus, 1758), Black Stork *Ciconia nigra* (Linnaeus, 1758), and Eurasian Crane *Grus grus* (Linnaeus, 1758). Counting these species requires very little additional effort from counters, while the information collected may help to monitor the precarious conservation status of these species in the east African-Palearctic migration system.

In this paper we describe the BRC dataset, which for the occasion of the 10th anniversary of the BRC was made publicly available through the Global Biodiversity Information Facility (GBIF) at https://www.gbif.org/dataset/d19c0287-15ee-45fd-b810-d30e8026a785. We describe our study site and the local flight paths and strategies of different species, elaborate on the count protocol used by our volunteer counters, and explain our data management strategy. We also discuss potential pitfalls for users and provide useful scripts (https://bitbucket.org/batumiraptorcount/gbif-data) to process count data for trend analyses. In our opinion, migration count data should always be published with open access to build a collaborative raptor migration monitoring network across all African-Palearctic flyways. More generally, we hope our dataset will reinforce the appreciation of the global importance of the eastern Black Sea flyway for migrant birds. Our transparent and open research approach should stimulate regional policymakers in particular to undertake urgent conservation actions regarding the still widespread practice of illegal raptor shooting along the Georgian Black Sea coast (Magnin 1989; Van Maanen et al. 2001; Abuladze et al. 2011; Jansen 2013; Sandor et al. 2017).

The global importance of the Batumi bottleneck

Since 2008, 35 species of raptors have been recorded at Batumi and more than one million raptors have been counted annually since 2012. After the first two years of pilot counts in 2008 and 2009, we compared annual species totals with global breeding bird population estimates of BirdLife International to assess the global importance of the Batumi bottleneck (Verhelst et al. 2011). Count procedures were further improved based on field experience gained during pilot counts and since 2011 counts have been made with consistently high effort each year. Based on these high-quality counts, we can now estimate annual counts separately across age groups, and compare the most recent breeding bird population estimates of BirdLife International (2018) to counts of adult birds for several target species (Table 1).

Table 1. Reassessing the global importance of BRC migration counts for target species based on high-quality data 2011–2018. Counts after 2011 were higher for most of these species due to improved count locations and seasonal coverage. Thanks to a large ageing effort we can now estimate annual abundance of adult raptors from total annual species counts corrected for unidentified birds, and these exceed 1% of the estimated world breeding population estimate for eight species and one subspecies. Calculations of annual totals per species and age group are explained further in this manuscript.

Species	Average count			World population estimate [2]	Percentage at Batumi (2011–2018)
	All individuals (2008–2009) [1]	All individuals (2011–2018)	Adult individuals (2011–2018)		
European Honey-buzzard	453,344	530,568	499,493 [3,4]	280,000–420,000	119–178
Steppe Buzzard	257,829	296,030 [5]	–	4,000,000	7 [6]
Black Kite	83,139	136,953	95,025 [3,4]	1,000,000–2,499,999	4–10
Lesser Spotted Eagle	4,794	7,715	3,153	40,000–60,000	5–8
Greater Spotted Eagle [7]	148	464	168	3,300–8,800	2–5
Steppe Eagle [7]	332	568	62	50,000–75,000	< 0.1
Booted Eagle	4,144	6,475	4,983	149,000–188,000	3
Short-toed Snake-eagle	675	1,427	887	100,000–200,000	< 1
Western Marsh-harrier	4,218	6,489	2,575	500,000–999,999	< 1
Montagu's Harrier	5,194	6,927	3,227	100,000–499,999	1–3
Pallid Harrier	1,652	1,491	376	18,000–30,000	1–2
Levant Sparrowhawk	4,668	3,508 [8]	–	10,000–19,999	18–35 [6]

[1] Verhelst et al. (2011), [2] BirdLife International (2018), for Steppe Buzzard (BirdLife International 2004), [3] based on separate age protocol (see chapter "Ageing raptors"), [4] including unknown amount of immature birds, [5] counts since 2012, [6] based on all individuals, [7] minimum number, migration period not fully covered, [8] experimental counts 2014–2017.

This reassessment strengthens our belief that globally important numbers of adult raptors pass through the Batumi bottleneck every year. The fact our counts of European Honey-buzzards exceed the largest global breeding population estimates (Table 1) indicates that the population must be far larger than currently estimated, especially considering that 10,000s of individuals breeding in Western and Central Europe migrate via other flyways.

Geography, weather, and flight paths of migrant raptors

Most raptors crossing the western half of the Greater Caucasus likely end up traveling across the Colchis Plains towards the Batumi bottleneck. The bottleneck is situated at the narrowest point between the eastern coast of the Black Sea and the foothills of the Lesser Caucasus, just to the north of the city of Batumi, in the Republic of Georgia (Fig. 1). Further inland, trans-Caucasian corridors are less well defined, but substantial numbers of raptors converge in large valleys and along watershed areas in both the Greater and Lesser Caucasus range, for example at Kazbegi (Tholin 2010), Mtkvari valley, Alazani, and the Javakheti Plateau (Abuladze 2013). In the eastern Caucasus an important bird migration flyway is situated along the west coast of the Caspian Sea in Azerbaijan, which is also used by substantial numbers of harriers and other raptors (Heiss and Gauger 2011). There is probably little exchange of soaring raptors between

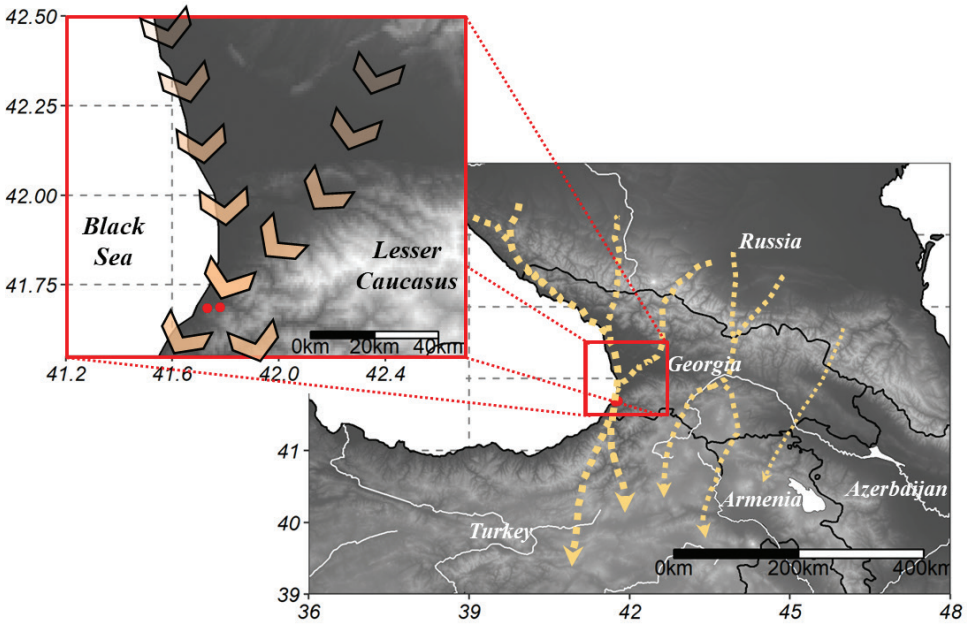

Figure 1. The Batumi bottleneck lies in the western coastal part of the trans-Caucasian migration corridor for soaring birds (main map, based on Abuladze 2013) and holds the strongest passage of migrant raptors at the eastern Black Sea flyway. The two hilltop count stations (red dots) are in the foothills of the Lesser Caucasus close to the city of Batumi in southwestern Georgia (inset).

these trans-Caucasian migration corridors and the eastern Black Sea flyway, within or between years, although this needs to be confirmed empirically, for example through tracking studies.

There is no clear geographical boundary that limits the bottleneck on the eastern side, and anecdotal observations and satellite tracking data even suggest species like Steppe Buzzard *Buteo buteo vulpinus* (Gloger, 1833) and Lesser Spotted Eagle *Clanga pomarina* (Brehm, 1831) may pass as far as 50 km inland. However, on most days, and especially during the first half of the count season, a land-sea breeze circulation produces strong cloud cover over the mountains in the afternoon, causing the local flight paths of raptors to shift towards the coast during peak mid-day migration activity. In the second half of the season there is usually less cloud cover in the mountains, and the passage of late migrants like Steppe Buzzard and Lesser Spotted Eagle within the bottleneck becomes less concentrated along the coast (Vansteelant et al. 2014).

The passage of migrant raptors at Batumi is affected by weather conditions at a regional scale. Long periods of sustained rainfall, which we detected based on satellite images of cloud cover, cause an accumulation of soaring raptors to the north of Batumi (Wehrmann 2012). Therefore, such long periods of adverse weather tend to be followed by a short period of outstanding migration passage. From Batumi onwards, soaring birds continue further south along the coast or further inland using, for example, the Chorokhi valley into North East Turkey (Andrews et al. 1977).

Count method

Count station

Migration counts are performed simultaneously from two count stations to cover the approximately 12 km long transect line. The two count stations are located on hilltops with unobstructed view facing north into the landscape, and within visible range from each other. Station 1 (41°41.0683'N, 41°43.815'E) oversees the coastal migration from the village of Sakhalvasho and is situated 2.4 km from the coast and at 324 m above sea level. Station 2 (41°41.22'N, 41°46.7583'E) covers migration across the mountainous side of the bottleneck from the village of Shuamta and is situated 4 km to the east of Station 1 and at 414 m above sea level. During the beginning of the first pilot count from 17 August 2008 to the end of September 2008, Station 2 was located slightly further north in Davituri and at a lower elevation (Station 2A: 41°41.665'N, 41°47.3117'E) where visibility towards the east was considerably poorer than at the location that has been in use since October 2008.

Obviously, the use of two stations introduces the unwanted possibility for birds to be double counted (i.e. recorded by counters on both stations), especially when they pass between the counting stations. Count teams minimize such double counts by avoiding records in the outer overlap zone and using intensive radio communication between the stations for the central overlap zone (Fig. 2). All birds are recorded with a classification of their distance relative to the count station. Combined with time of passage this distance information can be used to detect and remove any remaining double counts during data processing. Figure 2 shows a schematic overview of the distance zones and the relevant overlap areas.

From 2008–2011, we occasionally used a third count station in the village of Chakvistavi (41°40.73'N, 41°52.0183'E), situated 7.5 km east of Station 2. These counts were conducted mainly during the European Honey-buzzard migration and yielded low numbers of migrants compared to the other two count stations. Taken together with the high cost of counting at this remote location and the methodical difficulties of increased double counts, we decided on a count strategy using two count stations.

Count protocol

Information and experience gathered during the pilot counts in 2008–2010 guided the selection of target species for which we define priority and secondary species. For priority species, we expected long-term counts to generate relevant information for population monitoring. The selection of priority species is critical, because we determine our count season based on their phenology to ensure adequate monitoring.

In addition, we also target a number of secondary species that can easily be managed during counts of priority species because they pass in low numbers and are usually easily visible. These include enigmatic raptors like Short-toed Snake-eagle *Circaetus gallicus* (Gmelin, 1788) and Osprey *Pandion haliaetus* (Linnaeus, 1758), threatened species

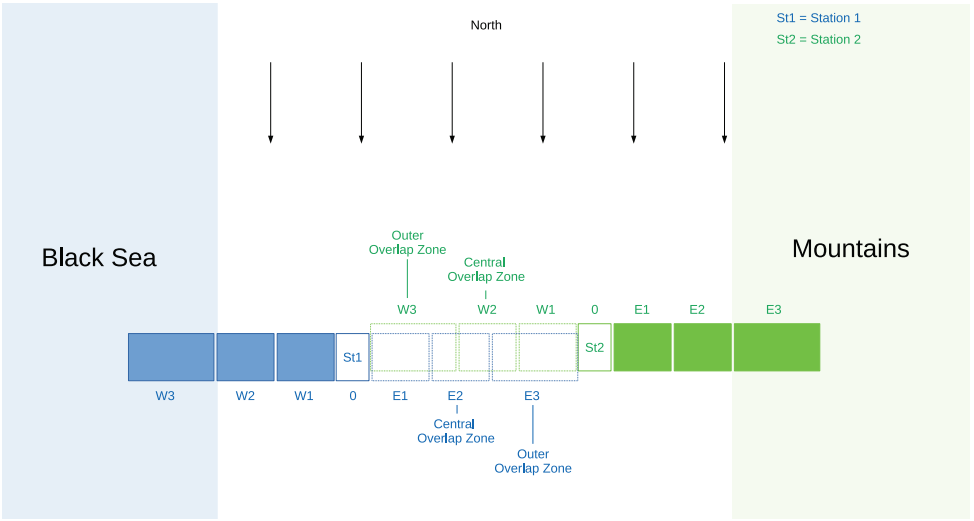

Figure 2. Schematic overview of distance and overlap zones of the two count stations at BRC showing the distance codes relative to the station from West3 (W3) to overhead (O) and East3 (E3).

like Egyptian Vulture *Neophron percnopterus* (Linnaeus, 1758) and Saker Falcon *Falco cherrug* (Gray, 1834), and some enigmatic or threatened non-raptors like European Roller, pelicans *Pelecanus* spp. and storks. In contrast to priority species, however, we do not modify our count season in function of the phenology of these species.

Unfortunately, not all birds can be identified to species level in the field. Such birds are then categorized as accurately as possible into morphological groups (Table 2). To estimate the number of each priority species in each of these groups we need to account for all potentially confusing species (see full procedure under Pitfalls and recommendations). Consequently, the list of secondary species was extended with all species that are easily confused with priority species e.g. Hen Harrier *Circus cyaneus* (Linnaeus, 1766), Greater Spotted Eagle *Clanga clanga* (Pallas, 1811), and Steppe Eagle *Aquila nipalensis* (Hodgson, 1833).

Targeting species entails that count-coordinators prioritize adequate counting of these species over others. For example, they ensure that sufficient people are counting flocks of priority and secondary species and scanning for birds even when a charismatic rarity passes by the station or when counters are distracted by outstanding passage of non-target species. However, users should be aware that following the analyses of pilot counts by Verhelst et al. (2011), we discontinued standardized surveys for some species in 2011.

Duration of the count

We determined to organize daily counts from 17 August to 16 October based on the average phenology of the earliest and latest priority species during the counts of

Table 2. List of migratory species recorded at Batumi Raptor Count and the abbreviations used for each species. Column "status" highlights which species are considered as priority and secondary species. All other species are not counted in a standardized way and for some species the count was discontinued in 2011.

English name	Scientific name	Abbreviation	Status
Buzzards			
European Honey-buzzard	*Pernis apivorus*	HB	PRIORITY
Steppe Buzzard	*Buteo buteo vulpinus*	StepBuz	SECONDARY
Common Buzzard	*Buteo buteo*	CommonBuz	
Crested Honey-buzzard	*Pernis ptilorhynchus*	CrestedHB	
Rough-legged Buzzard	*Buteo lagopus*	RoughLB	
Long-legged Buzzard	*Buteo rufinus*	LongLB	
Kites			
Black Kite	*Milvus migrans*	BlackKite	PRIORITY
Red Kite	*Milvus milvus*	RedKite	
Eagles			
Lesser Spotted Eagle	*Clanga pomarina*	LesserSE	PRIORITY
Greater Spotted Eagle	*Clanga clanga*	GreaterSE	SECONDARY
Steppe Eagle	*Aquila nipalensis*	SteppeE	SECONDARY
Eastern Imperial Eagle	*Aquila heliaca*	ImperialE	SECONDARY
Golden Eagle	*Aquila chrysaetos*	GoldenE	
Booted Eagle	*Hieraaetus pennatus*	BootedE	PRIORITY
Short-toed Snake-eagle	*Circaetus gallicus*	ShortTE	SECONDARY
Osprey	*Pandion haliaetus*	Osprey	SECONDARY
White-tailed Sea-eagle	*Haliaeetus albicilla*	WhiteTE	
Harriers			
Western Marsh-harrier	*Circus aeruginosus*	Mar	PRIORITY
Montagu's Harrier	*Circus pygargus*	Mon	PRIORITY
Pallid Harrier	*Circus macrourus*	Pal	PRIORITY
Hen Harrier	*Circus cyaneus*	Hen	SECONDARY
Vultures			
Egyptian Vulture	*Neophron percnopterus*	EgyptianV	SECONDARY
Griffon Vulture	*Gyps fulvus*	GriffonV	SECONDARY
Eurasian Black Vulture	*Aegypius monachus*	BlackV	SECONDARY
Sparrowhawks and Goshawk			
Levant Sparrowhawk	*Accipiter brevipes*	LevantSH	
Eurasian Sparrowhawk	*Accipiter nisus*	EurasianSH	
Northern Goshawk	*Accipiter gentilis*	Goshawk	
Falcons			
Lesser Kestrel	*Falco naumanni*	LesserKes	
Common Kestrel	*Falco tinnunculus*	CommonKes	
Red-footed Falcon	*Falco vespertinus*	RedFF	
Eleonora's Falcon	*Falco eleonorae*	EleonoraF	
Merlin	*Falco columbarius*	Merlin	
Eurasian Hobby	*Falco subbuteo*	Hobby	
Lanner Falcon	*Falco biarmicus*	LannerF	SECONDARY
Saker Falcon	*Falco cherrug*	SakerF	SECONDARY
Peregrine Falcon	*Falco peregrinus*	Peregrine	SECONDARY
Non-raptors			
White Stork	*Ciconia ciconia*	WhiStork	SECONDARY
Black Stork	*Ciconia nigra*	BlaStork	SECONDARY
Eurasian Crane	*Grus grus*	EurasianCrane	SECONDARY
Demoiselle Crane	*Grus virgo*	DemCrane	SECONDARY
Great White Pelican	*Pelecanus onocrotalus*	WhiteP	SECONDARY
Dalmatian Pelican	*Pelecanus crispus*	DalmatianP	SECONDARY
European Roller	*Coracias garrulus*	Roller	SECONDARY
European Turtle-dove	*Streptopelia turtur*	TurtleD	SECONDARY
Common Wood-pigeon	*Columba palumbus*	WoodP	SECONDARY
Stock Dove	*Columba oenas*	StockD	SECONDARY

English name	Scientific name	Abbreviation	Status
Morphological groups			
Pernis spp.		Pernis_SPEC	
Buteo spp. / *Pernis* spp.		Buzzard_SPEC	
Large Eagle		LargeEAGLE	
Montagu's / Pallid / Hen Harrier		MonPalHen	
Circus spp.		Harrier_SPEC	
Eurasian / Levant Sparrowhawk		SparrowH_SPEC	
Sparrowhawk / Goshawk		SPH_Goshawk	
Large Falcon		LargeFALCON	
Hobby / Red-footed Falcon		Hobby_RedFF	
Common / Lesser Kestrel		Kestrel_SPEC	
Falco spp.		Falcon_SPEC	
Medium sized raptor		MediumRaptor	
Unknown raptor		Raptor_SPEC	
White / Black Stork		Stork_SPEC	

2008–2010. More specifically, we start three days before the 1% quantile passage data of Montagu's Harrier until three days after the 99% quantile passage date of Lesser Spotted Eagle only to be interrupted during thunderstorms or long spells of rain.

The daily count period starts at one hour after sunrise and ends two hours before sunset. These start and end times were based on (1) experience gathered during pilot counts, which showed that only a minor fraction of soaring birds pass outside this time window, (2) accessibility and transportation time to reach both count stations, and (3) the consideration that extending the count by an additional two hours imposes a heavy toll on the fitness of observers, especially in late August, when stations are occupied for up to twelve hours daily as it is.

However, with a growing network of local hosts and collaborators, we were eventually able to improve accessibility of and transportation to the count stations. We started conducting irregular experimental surveys at sunrise at Station 1 that revealed that a substantial proportion of daily harrier passage took place during early morning hours. Harriers can do this because they can rely on flapping-gliding flight during absence of favourable thermal conditions (Spaar and Bruderer 1997). Therefore, since 2015, we extend daily counts by counting from sunrise with minimum two counters on each station during main passage of Montagu's and Pallid Harrier from 27 August to 27 September. Moreover, since 2015, irregular non-standardized counts are often conducted until sunset. We flagged the standardized and non-standardized observations in the column "filter" in our dataset. See Flagging standardized and non-standardized observations for further information on how to separate these data.

Count coordination and data registry

Counts are conducted by experienced and less experienced bird watchers who volunteer to count at least for two weeks. Count coordinators screen, select, and schedule volunteers such that each station can be staffed by a team consisting of one

coordinator and six to twelve counters, depending on migration intensity, diversity, and also counter availability. The team composition is equally balanced in terms of experience between both stations to be able to properly monitor the migration. The coordinator instructs the method of data recording, delegates tasks to the counting-team, communicates with the coordinator at the other station, and validates the data at the end of the day.

Migrants are recorded in the dataset within ten minutes after they have passed the transect line. For harriers, falcons, rollers, doves, and pigeons the data is recorded within five minutes. This avoids long uninterrupted counts, enabling us to study daily migration dynamic in more detail, and allows correcting for double counts between the two stations (see Data processing). Each record includes identification, distance zone relative to station, time, and for several species information on age, sex, and morph.

Note that in this way a single record can represent a solitary individual or an entire flock or stream, but also a subset of a larger flock or stream, as birds of different age, sex, or morph are recorded separately. At times of intense migration observations of solitary individuals passing a station in the same distance zone may be accumulated over several minutes and entered as a single record. Numbers associated with each record therefore do not represent group sizes.

Alternative count strategy for European Honey-buzzard

European Honey-buzzard migration is characterized by its great intensity involving large streams of birds passing between both stations, sometimes going on uninterrupted for hours, which makes it hard for counters to separate streams from each other. We therefore count European Honey-buzzard predominantly from Station 1 during its main migration from 21 August to 9 September. During this period few other species mix with European Honey-buzzard in streams and good visibility at this time of the year usually allows us to count even the most inland streams from this station. Occasional records from Station 2 in the database were collected when poor visibility prohibited a single-station count. Any double counts resulting from this approach are eventually removed as for other species according to an automated procedure described later in this paper (see Double count removal).

Identification of raptors using photography

Digital photography has become an important tool to aid identification of easily confused species such as adult and immature Greater Spotted or Steppe Eagle, adult Eastern Imperial Eagle *Aquila heliaca* (Savigny, 1809), female Pallid Harrier, and Crested Honey-buzzard *Pernis ptilorhynchus* (Temminck, 1821). Photography of difficult species has regularly been used for birds under poor visibility, or with inconclusive moult features.

Ageing raptors

Most raptors can be aged and often sexed, based on morphological features (Forsman 2003, 2016). We collect age information for as many birds as possible. For the three most numerous species, European Honey-buzzard, Steppe Buzzard, and Black Kite *Milvus migrans* (Boddaert, 1783), we sample daily age distributions for only a subset of birds.

European Honey-buzzard, Black Kite, and Steppe Buzzard
For European Honey-buzzard, Steppe Buzzard (only 2013), and Black Kite we use separate age protocols by sampling individuals rather than recording all birds as accurately as possible. These age protocols are restricted to birds passing between West1 (W1) to East1 (E1) of either count station. Second calendar year European Honey-buzzards are extremely rare in Europe and older immatures are impossible to distinguish from adults in the field. European Honey-buzzards overwinter in sub-Saharan Africa, and very few immatures come back to Europe with adults during their second calendar year (Corso 2012). In Batumi one record of a photographed second-calendar-year individual exists from autumn 2016 (Wright et al. in press). For immature Black Kites the determination of age in flight is challenging when large numbers pass the transect line in short time. We decided to monitor quantity rather than all age classes. Thus, for all three species, we only distinguish juvenile and non-juvenile birds. This data is recognizable by their abbreviations in the species column (HB_JUV, HB_NONJUV, BK_JUV, BK_NONJUV, SB_JUV, and SB_NONJUV).

Harriers
Ageing of female Harriers can be challenging and distant birds can be hard to distinguish from juvenile birds under poor visibility. Thus, we record birds as female colored, when they appear to be either in juvenile or female plumage. As it is often easier to determine age than to identify species for ringtail-harriers, we only trust records of Pallid and Montagu's Harrier if they also include age information. Records without age information were therefore reclassified during data processing into the broader category "MonPalHen" (see Table 2).

Large eagles
To reliably distinguish large eagles such as Lesser Spotted Eagle, Greater Spotted Eagle, Steppe Eagle, and Eastern Imperial Eagle it is essential to first determine their age (Forsman 2003, 2016). We require age information for all large eagles for thorough identification. In contrast to harriers, however, we are not able to record every single Lesser Spotted Eagle observation with age information in the dataset on days with intensive migration, but we ensure on the station they have been correctly identified. Finally, subadult large eagles in their fifth calendar year can be hard to distinguish from older adults and are therefore always recorded as adult.

Color morphs

Booted Eagle

Although the Booted Eagle *Hieraaetus pennatus* (Gmelin, 1788) occurs in pale, dark, and intermediate morphs in Batumi, we only separate pale individuals from all non-pale (here called dark) individuals (Forsman 2003, 2016). Dark morph individuals represent 51.9% of all Booted Eagles at Batumi (n = 42,475). This number matches with the known west-east gradient in the occurrence of dark morph Booted Eagle, with 20% dark morph individuals among eagles breeding in Spain and 80% among those breeding in eastern Russia (Karyakin 2007).

Western Marsh-harrier

A small number of Western Marsh-harriers are dark morph individuals (0.4%, n = 47,274). We only record males of the dark morph and note that substantial numbers of dark morph individuals may pass unnoticed when visibility or lighting is poor, or when they pass at far distance from either station, or when they are female colored.

Experimental count of Levant Sparrowhawk and Red-footed Falcon

Although the migration pattern of Red-footed Falcon *Falco vespertinus* (Linnaeus, 1766) is interesting to monitor, and for Levant Sparrowhawk *Accipiter brevipes* (Severtsov, 1850) pilot counts have confirmed globally relevant numbers in Batumi (Verhelst et al. 2011), we decided to do only an experimental count for these species, avoiding counting the potentially confusing species such as Eurasian Hobby *Falco subbuteo* (Linnaeus, 1758) and Eurasian Sparrowhawk. The experimental survey was performed from 2014 to 2017. To avoid the very effortful count of predominantly solitary migrating Eurasian Sparrowhawk and Eurasian Hobby, Levant Sparrowhawks and Red-footed Falcons were counted only in flock sizes of five or more individuals, without determining age and sex. Methodical challenges resulting in low quality data made the data insufficient to monitor trends, and thus, we did not continue these counts.

Steppe Buzzard

Following the pilot counts of 2008–2009 we initially decided not to monitor Steppe Buzzard at Batumi because we know large numbers of this species migrate over the interior of Georgia (Tholin 2010; Abuladze 2013) and because the migration of several priority species peaks during the Steppe Buzzard migration, which increases the counting effort. However, experience taught us that volunteer counters find it extremely demotivating not to count such a numerous migrant. Moreover, including this species formally in the count increases the possibility of reaching a million raptors per year. So, to help expand our international pool of potential volunteers, we resumed Steppe Buzzard counts in 2012.

Data on illegal shooting

Because illegal shooting has a relevant impact on several migrant species in Batumi, we record data on health conditions as either injured or killed. This data helps to quantify illegal shooting per year and species (Jansen 2013; Sandor et al. 2017).

Data management

The efficiency of data recording and management greatly improved over the years (Fig. 3). From 2008 to 2010 we took field notes on paper that afterwards had to go through the error prone and time consuming process of manual digitization. In 2011 we switched to handheld computers with a database entry module (palmtops), using paper notes in case of battery failure. In 2015, we changed to the mobile application of trektellen.org, which was partly developed based on the protocol and field experiences at Batumi Raptor Count.

During moderate quality check count-coordinators go quickly through the records to check for major errors (using simple criteria such as large flocks of rare birds, or specific age and sex combinations), and where possible correct them by discussing these observations with the relevant count team. Observations that are suspect due to insufficient information (e.g. a Greater Spotted Eagle cannot be identified without being aged) are degraded to a less specific level (in this example, to large eagle).

From 2011 onwards, count data were downloaded daily from palmtops to a project computer. Daily totals were then computed and entered manually in the online database of trektellen.org to provide daily updates to the general public. Part of the moderate data quality check and the upload of count data to trektellen.org were finally automated in 2015 with the transition to the trektellen.org application. This application partly validates most of the records before entry by asking users for missing data in obligate fields or alerting users to incompatible information in species identification, sex, and age fields. An example of the main record-screen is shown in Figure 4.

Data processing

Intensive quality check

Regularly during the season assigned data technicians run an intensive search for errors in the dataset based on the same features that count-coordinators use for validation during the daily moderate quality check. As this process is very time consuming our experience has shown that count-coordinators usually do not identify all data errors during their daily routine. This process is completed by an automated script procedure that ensures final count protocol integrity and degrades records to a less specific level if still insufficient information is detected.

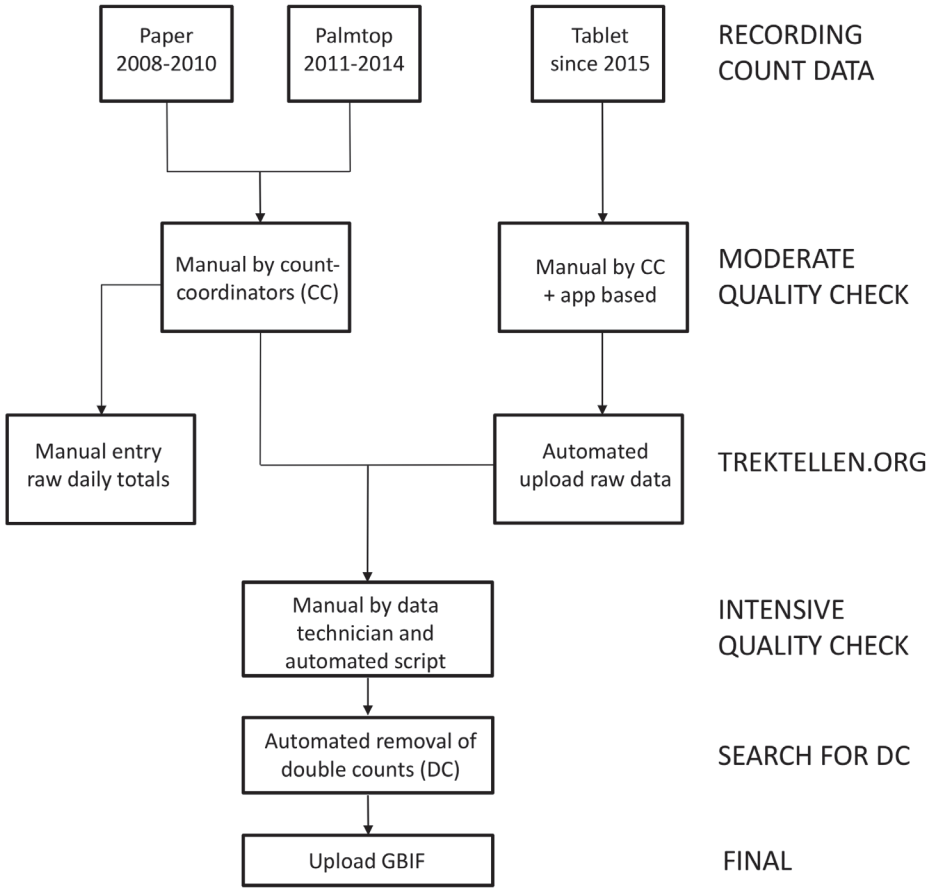

Figure 3. Diagram of data management and processing at BRC showing the data registry development from paper based entries in the beginning to the mobile application supported entries since 2015 with subsequent final data processing and upload to the GBIF database

Double count removal

An important final step in the production of the GBIF data product is to detect all remaining double counts in the overlapping count zones between the two stations. An automated procedure written in R detects potential double counts (on average 19,683 individuals annually) in different spatial and temporal windows for different species. In general, we distinguish between smaller and larger species because of differences in the distances at which they can be detected (spatial component) and differences in their flight behavior (temporal component). As a result, for smaller species such as falcons and harriers we consider double counts in a more narrow spatial overlap zone and a shorter time window than for larger species because the latter (e.g. eagles and buzzards) are visible from farther away. Soaring birds also take more time to pass through the bottleneck compared to actively flapping harriers, falcons, and sparrowhawks. To find

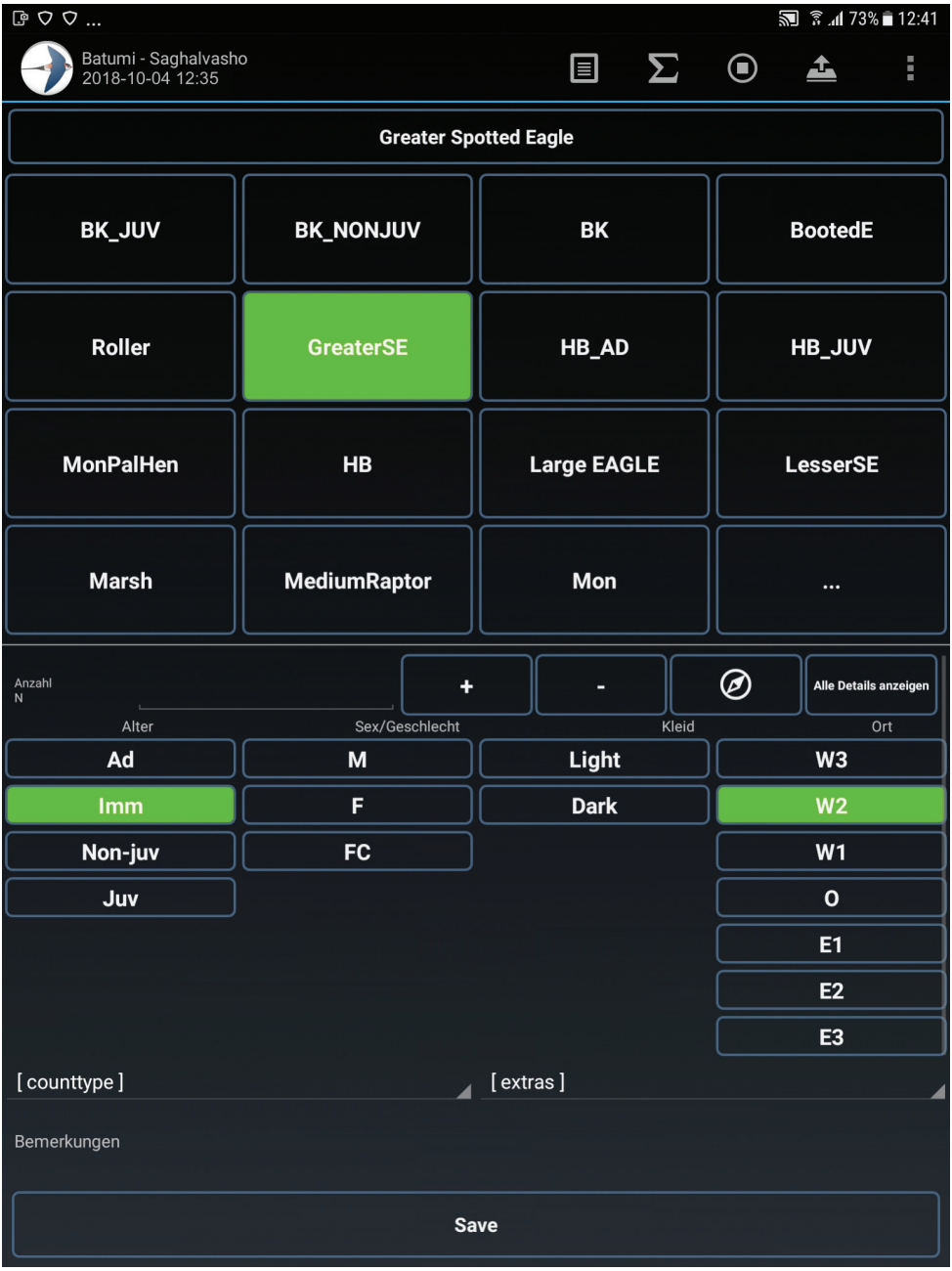

Figure 4. Screenshot of trektellen.org mobile application with the specific screen mode for raptor count at BRC.

the most suitable time frame in which double counts occur, we flagged known double counts in the field and found that most double counts are recorded within ± ten minutes at both stations in case of smaller and ± fifteen minutes in case of larger species.

We consider potential double counts not only within species, but also for corresponding higher orders of morphological groups. When a double count is detected, the observation with more details is kept. For example, three juvenile Pallid Harriers from Station 1 overlap with a record of eleven MonPalHen from Station 2, then the record of Station 1 has more details and is kept, while the record of Station 2 is subtracted by three. However, counters may flag records specifically as "single count" to exclude them of double count detection, if correctness is ensured through radio communication. On the other hand, a few recognized double counts are regularly and on purpose flagged as "double count" by observers to integrate them in the quality control of the detection script.

The double count approach is conservative, e.g. it detects more records as double counts than needed. As a result our data estimates the minimum number of individuals passing the bottleneck. However, double counts constitute less than 1% of all records, and so we do not expect double count removal to introduce any major bias in our data. For transparency the R-script for automated removal of double counts is available open access through the BitBucket account of the BRC (https://bitbucket.org/batumiraptorcount/gbif-data).

Flagging standardized and non-standardized observations

The dataset includes observations since 2011 for counts with standardized high quality observations (dataset column "filter" = 1), standardized early-morning counts of harriers conducted since 2015 (dataset column "filter" = 2), non-standardized observations from outside the seasonal and daily count period since 2011, or from pilot counts in 2008–2010, or from experimental counts (dataset column "filter" = 0). For most research purposes it is advised to only use the standardized observations.

Results

Final GBIF product: BRC migration counts since 2008

The entire reviewed and processed dataset is published open access in GBIF at https://www.gbif.org/dataset/d19c0287-15ee-45fd-b810-d30e8026a785 and will be updated annually after each season. Table 3 provides detailed column descriptions of the final data product. The dataset up to 2018 includes over 400,000 observation records from standardized, pilot, experimental, and irregular counts. Table 4 provides processed year totals of all target species and their corresponding morphological groups since 2011 excluding non-standardized records. Table 5 shows the positive effect on total numbers of harriers since the recently integrated early morning counts have been started. The totals for all raptors (Table 6), including standardized and non-standardized species records, reach over one million raptors at the Batumi bottleneck every year during autumn migration.

Table 3. Detailed column description of the final GBIF product of BRC.

Column	Content
id	consecutive number
date	YYYY-MM-DD
time	hh:mm:ss
species	abbreviation of species or higher order of morphological groups (see Table 1)
number	processed number of migrants excluding double counts
north	number of migrants going north
station	number of the station, values: 1, 2
location	distance zone, values: W3, W2, W1, O, E1, E2, E3, E4
age	values: ad = adult, imm = immature, nonjuv = non-juvenile, juv = juvenile
sex	values: f = female, fc = female coloured (either juv or f), m = male
morph	values: dark, light, ful = fulvescens, mel = melanistic, leu = leucistic
health	health condition: kil = killed, inj = injured
remark	text with additional informations
dcremark	shows the corresponding record ID of the associate double count record with the concurrent number that is either subtracted (-) or kept (+)
filter	0 = non-standardized, 1 = standardized, 2 = standardized early morning count

Table 4. Year totals of all target species and their corresponding morphological groups based on standardized species records during autumn migration (dataset column "filter" = 1).

Species	2011	2012	2013	2014	2015	2016	2017	2018
European Honey-buzzard	370,587	643,212	427,183	656,171	559,790	509,112	518,242	485,917
Steppe Buzzard	–	185,317	415,439	486,467	199,620	203,210	281,403	300,757
Buzzard_SPEC	2,054	178	184	217	0	1,732	0	15,621
Black Kite	80,206	101,279	104,374	104,669	118,466	163,239	159,161	149,077
Lesser Spotted Eagle	5,844	4,536	3,845	2,467	4,088	3,721	4,696	4,278
Greater Spotted Eagle	220	160	203	243	397	273	331	426
Steppe Eagle	183	165	348	260	477	249	271	437
Eastern Imperial Eagle	37	11	37	46	33	29	44	62
Booted Eagle	6,497	7,001	6,150	6,143	6,639	7,370	6,814	5,188
Short-toed Eagle	1,293	1,348	1,376	1,405	1,329	1,443	1,436	1,788
Osprey	122	80	147	103	136	143	119	129
LargeEAGLE	2,646	2,390	6,446	7,256	2,404	1,967	3,417	5,343
Western Marsh-harrier	5,084	5,526	7,597	7,036	7,296	5,523	6,422	7,334
Montagu´s Harrier	2,753	5,010	3,245	2,802	2,997	2,506	2,967	1,794
Pallid Harrier	365	801	747	838	702	358	1,553	495
Hen Harrier	6	19	16	41	29	5	36	40
MonPalHen	4,314	6,650	5,398	5,892	5,103	2,994	2,212	4,907
Harrier_SPEC	32	10	30	15	6	33	22	38
Egyptian Vulture	40	24	36	19	27	28	19	17
Griffon Vulture	2	1	9	9	1	4	4	3
Eurasian Black Vulture	1	0	0	0	1	0	1	0
Lanner Falcon	1	0	0	0	0	0	0	0
Saker Falcon	2	1	1	3	2	1	0	1
Peregrine Falcon	31	48	28	32	40	26	26	22
LargeFALCON	14	11	5	1	6	1	1	8
MediumRaptor	9,774	14,722	160,557	32,124	53,303	45,299	36,231	92,104
Raptor_SPEC	0	0	0	0	0	3	277	428
White Stork	572	444	417	1,422	199	459	410	577
Black Stork	992	1,268	1,483	1,465	1,249	1,200	1,419	1,750
Stork_SPEC	0	10	25	0	0	0	0	14
Eurasian Crane	4	21	42	114	212	26	100	165
Demoiselle Crane	0	0	0	0	0	0	0	0
Great White Pelican	0	0	0	0	2	0	0	0
Dalmatian Pelican	0	0	3	0	0	2	0	0
European Roller	1,253	1,778	1,477	2,161	450	1,159	702	922
European Turtle-dove	–	–	4,571	1,099	461	1,934	1,714	686
Common Wood-pigeon	–	–	402	1,580	32	450	157	292
Stock Dove	–	–	1,300	764	800	765	387	713

Table 5. Year totals of harrier species based on standardized species records during autumn migration including standardized early morning counts since 2015 (dataset column "filter" = 1 and 2).

	Including early morning counts				Additional proportion (%) from early morning counts			
	2015	**2016**	**2017**	**2018**	**2015**	**2016**	**2017**	**2018**
Western Marsh-harrier	8,458	6,111	7,418	8,081	16	11	16	10
Montagu's Harrier	3,262	2,781	3,591	1,938	9	11	21	8
Pallid Harrier	748	364	1,721	517	7	2	11	4
Hen Harrier	29	6	36	41	-	-	-	-
Mon / Pal / Hen Harrier	5,589	3,453	3,128	5,447	10	15	41	11
Harrier spp.	8	58	36	93	-	-	-	-
Total	**18,094**	**12,773**	**15,930**	**16,117**	**12**	**12**	**21**	**10**

Table 6. Year totals for raptors between 2008 and 2018 based on standardized (dataset column "filter" = 1 and 2) and non-standardized (dataset column "filter" = 0) species records. More than 1 million raptors have been registered during autumn migration in Batumi every year since 2012.

Dataset column filter	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**
1	-	-	-	492,118	978,528	1,143,468	1,314,297	962,947	949,305	1,025,735	1,076,244
2	-	-	-	-	-	-	-	1,961	1,354	2,718	1,509
0	881,838	917,119	504,825	1,739	31,428	56,294	36,500	65,761	92,939	26,031	53,767
Total	**881,838**	**917,119**	**504,825**	**493,857**	**1,009,956**	**1,199,762**	**1,350,797**	**1,030,669**	**1,043,598**	**1,054,484**	**1,131,520**

Pitfalls and recommendations for analyses

Anyone using the GBIF data product is encouraged to contact the BRC team (research@batumiraptorcount.org) to discuss potential pitfalls for their specific usage. We here make some general recommendations for how to deal with known pitfalls that will commonly affect all researchers planning to use BRC count data.

Using data directly from trektellen.org is discouraged, as this only presents totals based on raw data excluding complete data checks and correction for double counts. The trektellen.org dataset includes non-standardized records such as irregular observations of non-target species, birds counted outside standardized count periods, and pilot or experimental counts. We strongly recommend to only use the standardized records in the GBIF dataset by filtering all records with value = 1 in the column "filter", and following the recommendations below to calculate daily and annual totals for each species.

Correct for unidentified birds (UID) in estimation of daily species totals

Raptors can be difficult to identify especially when large streams of soaring migrants pass in the far east or west of the bottleneck or when visibility is poor. In such cases birds are more often identified to general morphological groups. In particular for ringtail-harriers, more birds are identified to the level of their morphological group

(MonPalHen) than to actual species level. To include these unidentified birds in daily species totals for each higher morphological group, we estimate the daily proportion of the corresponding species, recalculate the daily total of that morphological group into species fractions, and add those to the daily totals of identified birds. We developed a script that iterates this procedure according to nested morphological groups used on the count stations (Fig. 5). For example, to estimate the daily total of European Honey-buzzard (HB), we must calculate how many of the birds recorded as Buzzard-SPEC, MediumRaptor, and Raptor-SPEC were likely to be HB. To do this, we first calculate the daily proportion of HB among all buzzards to estimate the number of HB in the category Buzzard-SPEC. We then add this number to the daily total of HB, recalculate proportion of HB among all buzzards and kites to estimate the number of HB in the category MediumRaptor. Finally, we estimate the daily proportion of HB among all raptors to estimate the number of HB in the category Raptor-SPEC.

An R script to estimate daily species totals (including and excluding UIDs) from the final GBIF data product described in this paper is made available through the BRC BitBucket account (https://bitbucket.org/batumiraptorcount/gbif-data). This script will read the GBIF dataset and produce a table with daily totals for each species. In case users run into difficulties with this script, the resulting table is available upon request by the BRC (research@batumiraptorcount.org).

Using data about age, sex and morph

The number of birds for which detailed age and sex information can be recorded varies greatly, not only depending on intensity of migration, but also on experience and effort of volunteer observers. This also applies for European Honey-buzzards and Black

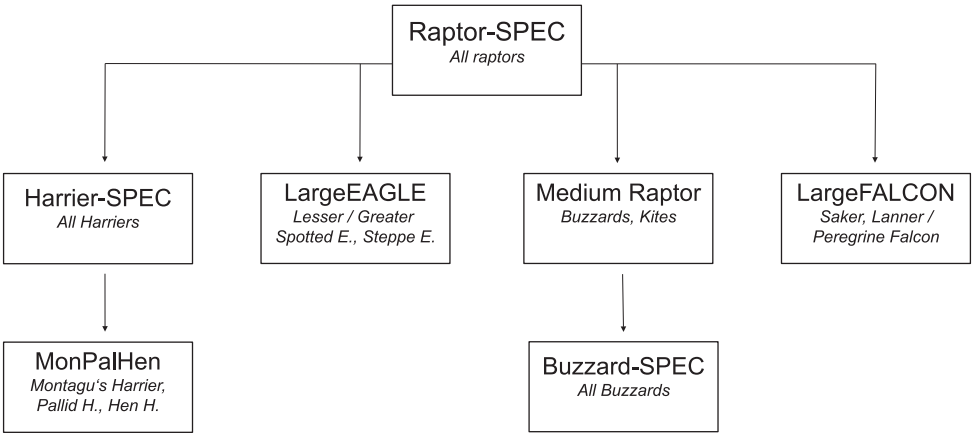

Figure 5. Hierarchy of morphological groups used to estimate how many "unidentified birds" belong to each species level shown only for target species at BRC.

Kites with their specific (separate) ageing protocol. Records with information on age, sex, or other plumage features, therefore, cannot be used directly to detect age-, sex-, or morph-specific migration strategies and trends. However, daily proportions of age groups, sexes, and/or morphs within the subset of accurately identified birds can be used to estimate daily totals of these groups from daily species totals (including the recalculation of morphological groups).

For European Honey-buzzards and Black Kites, we strongly recommend not estimating daily proportions of age groups and sexes from records in the regular count protocol (species values HB, BlackKite) but from the designated age protocol only (see Ageing raptors).

Trend analyses

Data are likely not useful for trend analyses in species for which annual totals do not exceed 50–100 individuals (e.g. vultures, large falcons), species that have not been a target of the project, and species for which the count data does not cover the entire migration period (Greater Spotted Eagle, Steppe Eagle, Hen Harrier). Moreover, we strongly recommend analyzing standardized data only from 2011 onwards, when a fully-fledged count protocol was initiated.

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