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Research article

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Species turnover between the northern and southern part of the South China Sea in the *Elaphropeza* Macquart mangrove fly communities of Hong Kong and Singapore (Insecta: Diptera: Hybotidae)

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Abstract. A recent survey of the mangroves around Hong Kong revealed the presence of seven species of the genus *Elaphropeza* Macquart, 1827. All belong to a group of yellow species that occur exclusively in mangroves. Three species were previously known: *Elaphropeza calcarifera* Bezzi, 1912 and *E. xanthocephala* Bezzi, 1912, both from Taiwan, and *E. riataiae* Shamshev & Grootaert, 2007 from Singapore. Four species are new to science: *Elaphropeza furcatella* sp. nov., *E. guenardi* sp. nov., *E. hongkongensis* sp. nov. and *E. hongshulin* sp. nov. All seven species are described or an extended diagnosis is provided. All species are figured and NGS barcodes are made available. A key is given for the Hong Kong species and their siblings from Singapore and Taiwan. Remarkable is that five of the seven species are more or less closely related to species occurring in Singapore. Genetic distances and morphologic differences are congruent. The species turnover between the northern part and the southern part of the South China Sea is high, with only one of the seven species present in both regions.

Keywords. Mangrove, *Elaphropeza*, species turnover.

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Introduction

As was shown in a long-term survey of the mangrove fauna of Singapore (Grootaert & Shamshev 2012), the hybotid flies, and especially the species of *Elaphropeza* Macquart, 1827, are very diverse in mangroves. Here, the relationship is examined between the fauna recorded in Singapore situated in the southern part of the South China Sea and Hong Kong situated at about 3000 km north in the northern part of the South China Sea. Do the same species or species groups occur over the South China Sea mangroves and what is the species turnover?

Singapore is situated near the equator at 1° N and has a humid tropical climate. There are two monsoonal periods with rains from March to June, dryer in July and August, resuming rain from September onward and sometimes very humid in January followed by very little or no rain in February (Meteorological Service Singapore 2019). Being an island on the equator, the average temperature is the same throughout the year with 32°C during the day and 24°C at night. The mangrove flora is diverse with nineteen species of true mangrove trees (Yang *et al.* 2011; Ng & Sivasothi 1999).

Hong Kong is situated at 22° N and thus at a much higher northern latitude. It has a seasonal subtropical climate and the seasons are more marked with a ‘winter and a summer period’. Climate and weather information are available from the Hong Kong Observatory (2017). Mangroves reach their northern distribution limit in Hong Kong and they are composed of only eight mangrove tree species, among them *Bruguiera gymnorhiza* or large-leaved orange mangrove is fairly common.

Elaphropeza is a genus of small leaf-dwelling predatory flies that thrives in the tropics. It is distributed worldwide with about 220 known species (Yang *et al.* 2007; Shamshev & Grootaert 2007; Grootaert & Shamshev 2012). The species from the Chinese mainland were reviewed by Yang & Gaimari (2005) who also provided a key. The Oriental species were revised by Shamshev & Grootaert (2007) and Grootaert & Shamshev (2012, 2015). Yang *et al.* (2006) revised species of *Elaphropeza* from neighbouring Guangdong Province in China, where they found three species: *Elaphropeza chebalingensis* Yang, Merz & Grootaert, 2006, *E. guiensis* (Yang & Yang, 1989) and *E. plumata* Yang, Merz & Grootaert, 2006. Recently, the fauna of Taiwan was revised by Wang *et al.* (2012), where they recorded fourteen species with a key to the species of Taiwan.

All Hong Kong species were NGS-barcoded (313 bp) following the technique described in Meier *et al.* (2016), so that cryptic species became visible and females, which are usually very difficult to identify based on morphological characters, could be linked to the corresponding males. Specimens of *Elaphropeza riatanae* Shamshev & Grootaert, 2007 showed a high variation in the colouration of the scutellum, which is a key character to identify species of *Elaphropeza*. The barcodes did not support this variation, indicating that all specimens were conspecific.

Material and methods

A survey was made in autumn 2017 with Malaise traps at 22 mangrove sites all around Hong Kong (C.Taylor, U. Chang and B. Guénard) (Fig. 1). The traps were operational during 2 weeks per site. Most of the stations were back mangroves and only a few front mangroves. Each station received a code, e.g., 5BM1 in which 5B refers to the station and M1 to the first period that the trap was operated at that station.

All specimens were conserved in 70% ethanol. Holotypes and paratypes are conserved in the collections of the Royal Belgian Institute of Natural Sciences in Brussels (RBINS). Voucher specimens are deposited in the Natural History Museum of the University of Hong Kong (HKU) and the Lee Kong Chian Natural History Museum in Singapore (LKCNH).

The Hong Kong specimens were NGS-barcoded (313 bp) at the National University of Singapore following the techniques described in Meier *et al.* (2016) and Wang *et al.* (2018) in a cost effective and non-destructive way (Wong *et al.* 2014) allowing females to be matched with males (Yeo *et al.* 2018) Their reference code starts with HKC followed by a number. A few specimens were handled by Ms Jayanthi Puniamoorthy using the classic technique (630 bp) and their reference code starts with JP.

The Singapore species were barcoded at RBINS in Brussels as described in Nagy *et al.* (2013). Their reference code starts with AB followed by a number. These barcodes are available from GenBank.

Estimates of Evolutionary Divergence between sequences were conducted in MEGA7 (Kumar *et al.* 2016; Tamura *et al.* 2004). The number of base substitutions per site between sequences are shown. Analyses were conducted using the Maximum Composite Likelihood model. The analysis involved 78 nucleotide sequences. Codon positions included were 1st+2nd+3rd+Noncoding. All positions containing gaps and missing data were eliminated. There was a total of 295 positions in the final dataset.

The stacked habitus images were made according to Brecko *et al.* (2014). The morphology and terminology of *Elaphropeza* are described in Grootaert & Shamshev (2012). The male terminalia were removed, macerated, prepared on a microscopic slide in a gel so that the terminalia could be orientated in the same position and drawn with a camera lucida.

Abbreviations used are as follows:

- c = cercus (fused right and left cercus)
- e = epiproct
- lc = left cercus
- lel = left epandrial lamella
- ls = left surstyli
- rc = right cercus
- rel = right epandrial lamella



Fig. 1. Distribution of the Malaise traps around Hong Kong (map by C. Taylor and U. Chang).

Results

Class Insecta Linnaeus, 1758
Order Diptera Linnaeus, 1758
Superfamily Empidoidea Latreille, 1804
Family Hybotidae Macquart, 1823
Subfamily Tachydromiinae Meigen, 1822

Genus *Elaphropeza* Macquart, 1827

Elaphropeza Macquart, 1827: 86 (type-species: *Tachydromia ephippiata* Fallén, 1815, by monotypy).
Ctenodrapetis Bezzi, 1904: 351 (as subgenus of *Drapetis*) (type-species: *Drapetis* (*Ctenodrapetis*) *ciliatocosta* Bezzi, 1904 by subsequent designation in Melander 1928: 309).

The genus *Elaphropeza* can be distinguished from other genera of the Drapetidini by the following combination of characters: occiput convex, antennae not upturned, postpedicel conical, its ventral margin as straight as dorsal margin, stylus apical, anepisternum bare, wing with shortened cell br, abdominal tergites may bear squamiform setae, intersegmental modifications present between tergites 3–5 or 4–5. For a detailed diagnosis and the general morphology we refer to Grootaert & Shamshev (2012).

Key to male *Elaphropeza* from mangroves in Hong Kong

The present key is limited to the species occurring in mangroves in Hong Kong and their siblings in Singapore and Taiwan, modified after Grootaert & Shamshev (2012). All species belong to the *E. ephippiata* group in having the proepisternum bare just above the fore coxa (lacking a long upturned bristle) and the abdominal tergite 3 with unmodified setae, lacking squamiform setae.

All species here are yellow with an entirely yellow scutum without spots, with yellow or black occiput and hind tibia with a single anterodorsal bristle near the middle. Wings hyaline or uniformly infuscate.

For black species or those with hind tibia without prominent bristles or with an apical curved spine, or scutum with a colour pattern or wing with a pattern, check Grootaert & Shamshev (2012, 2015) for Oriental species or Yang *et al.* (2005, 2006) for China and Wang *et al.* (2012) for Taiwan.

1. Occiput black 2
- Occiput yellow (Taiwan, Hong Kong) *E. xanthocephala* Bezzi, 1912
2. Hind tibia with long pointed apical projection. Scutellum and metanotum brown. Acrostichal bristles lacking on prescutellar depression. Haltere yellow (Taiwan, Hong Kong) *E. calcarifera* Bezzi, 1907
- Hind tibia with short, rounded apical projection. Different combination of characters 3
3. Scutellum entirely yellow 4
- Scutellum largely brown or black (in *E. riatanae* there is a variation of colouration from entirely yellow to entirely brown to black scutellum, but metanotum is always black) 10
4. Acrostichal bristles extending to base of scutellum. Haltere darkened 5
- Acrostichal bristles lacking on prescutellar depression. Haltere yellow 6
5. Postpedicel about 6.0× longer than wide, stylus about 0.7× length of postpedicel. Right epandrial lamella with only two pale blunt spines. Tip of fused part of cerci long, with short bristles. Metanotum reddish-yellow (Singapore) *E. asiophila* Shamshev & Grootaert, 2007

- Postpedicel about 4.6× as long as wide, stylus nearly as long as postpedicel (0.86×). Tip of right epandrial lamella with 3 black blunt spines; fused part of fused cerci shorter, with long bristles (Fig. 7A–B). Metanotum rather orange-yellow (Hong Kong) *E. guenardi* sp. nov.
- 6. Fore tibia and tarsus, mid and hind tarsomere 5 brownish (legs sometimes entirely yellow in *E. furcatella* sp. nov.). Abdominal tergite 4 and 5 with or without squamiform setae 7
- Legs with only tarsomere 5 brown. Abdominal tergite 4 with slightly flattened setae, tergite 5 with squamiform setae 8
- 7. Abdominal tergites 4 and 5 with squamiform setae. Male: cerci broadly fused, right epandrial lamella truncate apically, lacking spines (Singapore) *E. furca* Shamshev & Grootaert, 2007
- Abdominal tergites 4 and 5 without squamiform setae. Male: tip of right epandrial lamella forked (Fig. 5A), tip of cercus truncate, but pointed at the left side (Fig. 5B). Legs entirely yellow, sometimes fore and mid tibiae and tarsi dusky yellow, not brown. *E. furcatella* sp. nov.
- 8. Male: right epandrial lamella with unmodified setation, lacking spines (Fig. 11F) (Singapore)
..... *E. lowi* Grootaert & Shamshev, 2012
- Male: right epandrial lamella with three apical black spines or a single subapical spine at the inside 9
- 9. Tip of right epandrial lamella broadened, with three black spines apically (Fig. 11E) (Malaysia, Singapore) *E. malayensis* Shamshev & Grootaert, 2007
- Tip of right epandrial lamella not broadened and bearing a single spinule at the inside (Fig. 11B) *E. hongshulin* sp. nov.
- 10. Scutellum brown medially (Taiwan) *E. marginalis* Bezzi, 1912
- Scutellum entirely brown or black 11
- 11. Legs with fore tibia and tarsus wholly brown, hind femur near apex above brownish (Singapore, Hong Kong) *E. riataiae* Shamshev & Grootaert, 2007
- Legs with only tarsomere 5 brown to black 12
- 12. Acrostichal bristles biserial near middle of scutum, lacking on prescutellar depression 13
- Acrostichal and dorsocentral bristles multiserial 14
- 13. Larger (about 2.5 mm). Left surstylus with a shallow notch apically (Grootaert & Shamshev 2012: fig. 155) (Singapore) *E. feminata* Shamshev & Grootaert, 2007
- Large (about 1.7 to 2.3 mm). Left surstylus with a deep notch on dorsal border (Fig. 9C) (Hong Kong) *E. hongkongensis* sp. nov.
- 14. Hind tibia with long, pointed apical projection; two long prescutellars (Taiwan, Hong Kong)
..... *E. calcarifera* Bezzi, 1907
- Hind tibia with small, rounded apical projection; one long prescutellar bristle (Taiwan)
..... *E. melanura* Bezzi, 1912

Elaphropeza calcarifera Bezzi, 1907
Figs 2–3

Elaphropeza calcarifera Bezzi, 1907: 488, male, type locality: Taiwan, Takao.

Elaphropeza calcarifera – Bezzi 1912: 489, female. — Shamshev & Grootaert 2007: 114, figs 188–190, re-description; neotype designated from Taiwan, Anping.

Material examined

HONG KONG • 1 ♂, 4 ♀♀; Shui Hau (19M1); 22.21936° N, 113.91898° E; C. Taylor and U. Chang leg.; 1–14 Nov. 2017; male dissected and figured (Fig. 3); RBINS • 2 ♂♂; Sam A Chung (5BM1); 22.50829° N, 114.27248° E; C. Taylor and U. Chang leg.; 11–27 Dec. 2017; both dissected and barcoded with references: JP2B, JP2C; both have yellow tergites 6 and 7; RBINS • 5 ♂♂, 1 ♀; Tai Tam (22M1); 22.24614° N, 114.22334° E; C. Taylor and U. Chang leg.; 9–23 Oct. 2017; with following NGS barcode references: HKC_0000787 ♀ 22M1, HKC_0000788 ♂ 22M1, HKC_0000789 ♂ 22M1, HKC_0000790 ♂ 22M1, HKC_0000791 ♂ 22M1, HKC_0000793 ♂ 22M1; RBINS • 3 ♂♂, 2 ♀♀; Tai Tam (22M2); 22.24614° N, 114.22334° E; C. Taylor and U. Chang leg.; 23–30 Oct. 2017; with following NGS barcode references: HKC_0000798 ♂ 22M2, HKC_0000800 ♂ 22M2, HKC_0000804 ♀ 22M2, HKC_0000808 ♂ 22M2, HKC_0000809 ♀ 22M2; RBINS.



Fig. 2. *Elaphropeza calcarifera* Bezzi, 1907, ♂, habitus, RBINS (leg. C. Taylor and U. Chang; photo A. Samoh).

Description

Male (Fig. 2)

BODY. 1.5 – 1.7 mm long; wing 1.3 – 1.4 mm long.

HEAD. Scape and pedicel yellow, postpedicel brownish, base largely yellow. Inner vertical bristles nearly twice as long as outer verticals. Postpedicel 3× as long as wide; stylus as long as postpedicel.

THORAX. Scutum yellow, scutellum and metanotum brown. Acrostichals irregularly tri- to quadri-serial, not reaching border of scutellum. Two longer prescutellars, distinct from other short dorsocentrals. Most apical one twice as long as the preceding one.

LEGS. Yellow, but tarsomere 5 of all legs contrastingly black. Mid femur ventrally with a single row of short spine-like bristles, not as long as femur is wide, bristles brown in basal half while pale in apical half. Mid tibia with short somewhat flattened bristles, not really spinules ending in indistinct pale short apical spine. A long pale preapical posterior bristle present. Hind tibia with long brown anterodorsal seta near middle.

WING. Clear, veins yellow; costal bristle yellow. Haltere white.

ABDOMEN. Tergites 1–3 yellow, tergite 4 large, shining black, lacking squamiform setae, tergite 5 very narrow, with a row of squamiform setae; tergites 6–7 yellow.

TERMINALIA (Fig. 3). Right epandrial lamella black, except for dusky yellow base. Cerci fused with pale brown digitiform tip, a strong bristle below middle (Fig. 3B). Left surstylius black, narrow with a truncate tip bearing yellow hairs, dorsal margin with a very long seta at base and a few strong setae near middle (Fig. 3C).

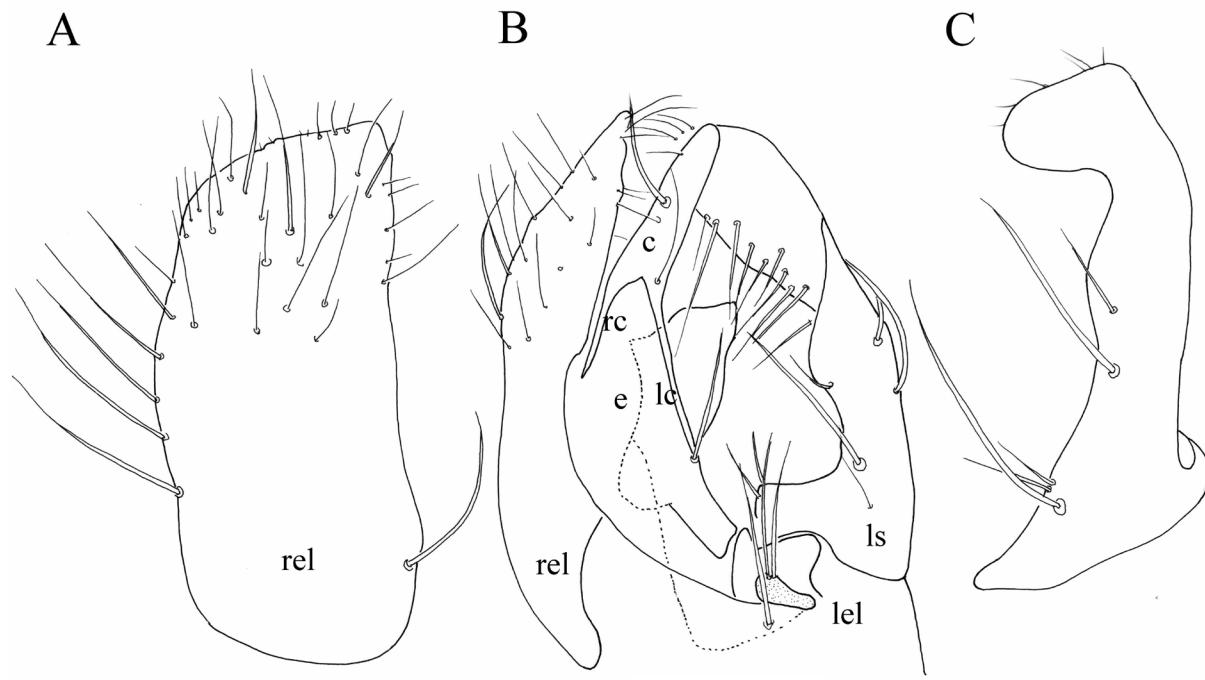


Fig. 3. *Elaphropeza calcarifera* Bezzi, 1907, male terminalia, RBINS (leg. C. Taylor and U. Chang). **A.** Right epandrial lamella. **B.** Epandrium, dorsal view. **C.** Left surstylius. Scale bar: 0.1 mm.

Female

BODY. 1.7 – 1.8 mm long; wing 1.4 mm long.

Identical to male in most respects. Stylus a little longer than postpedicel. Tergite 8 black, cerci very short, pale brown, tergite 8 long, brown, produced beyond the cerci. The ovipositor is quite large and on superficial look like male terminalia.

Remarks

The presence of a pointed apical projection in *E. calcarifera* on the hind tibia is easily overlooked and, therefore, this species is mentioned twice in the key above. When the pointed projection is overlooked, it will lead in the key to the Oriental *Elaphropeza* (see Grootaert & Shamshev 2012) *E. melanura* Bezz, 1912, also described from Taiwan. Unfortunately, the neotype male of *E. melanura* has not been dissected to illustrate the male terminalia. Apart from the pointed projections, the differences with *E. calcarifera* are small, but there are a few characters to distinguish the two species. In *E. melanura* the inner verticals are long, while the outer ones are hardly prominent. In *E. calcarifera* the inner verticals are also very long and the outer ones distinct and more than half as long as the inner ones.

In *E. melanuroides* Grootaert & Shamshev, 2015, another related species, the inner verticals are as long as the outer verticals. The postpedicel is brown in *E. melanura*, while in both *E. calcarifera* and *E. melanuroides* the postpedicel is brown with its base ventrally largely yellow. There is one long prescutellar bristle in *E. melanura*, while *E. calcarifera* and *E. melanuroides* have two longer prescutellars. The haltere is yellow in *E. melanura* while white in *E. melanuroides*. However, the colour of the haltere might have become yellow over time as it is a dried specimen. Both *E. calcarifera* and *E. melanuroides* were fresh in our study and have been studied in ethanol. The mid femur in *E. melanura* bears two rows of spine-like, short ventral bristles. In *E. calcarifera* there is only a single row of strong bristles. In *E. melanuroides* the mid femur has bristles that are not spine-like; however, on the apical third there are some darker bristles.

In *E. calcarifera* there is variation in the colour of tergites 6 and 7 from very pale to yellow and even dusky yellow.

Elaphropeza furcatella sp. nov.

[urn:lsid:zoobank.org:act:8DC272D2-7B30-4371-A22F-C437B77BBAA9](https://lsid.zoobank.org/act:8DC272D2-7B30-4371-A22F-C437B77BBAA9)

Figs 4–5

Etymology

The specific name is from the Latin ‘*furca, furcatella*’, meaning ‘fork, small fork’, and alludes to the fork-shaped tip of the right epandrial lamella.

Material examined

Holotype

HONG KONG • ♂; Tai Tan (28M1); 22.43857° N, 114.33327° E; C. Taylor and U. Chang leg.; 5–19 Dec. 2017; barcode reference JP1F (not dissected); RBINS.

Paratypes

HONG KONG • 1 ♀; same collection data as for holotype; barcode reference HKC_0000505; RBINS • 1 ♂; Tai Tam (22M2); 22.24614° N, 114.22334° E; C. Taylor and U. Chang leg.; 9–23 Oct. 2017; barcode reference HKC_0000801; RBINS.

Description

Male (Fig. 4)

BODY. 1.4 mm long; wing 1.5 mm long.

HEAD. Occiput black, scape and pedicel yellow, postpedicel brown, but paler on basal half. Postpedicel nearly 4× as long as wide. Stylus a little longer than postpedicel. Palpus yellow, with white basal and pale brown subapical bristle. Proboscis pale yellowish.

THORAX. Yellow, including scutellum, metanotum dusky yellow (not brown). Acrostichals quadri-serial, not reaching scutellum.



Fig. 4. *Elaphropeza furcatella* sp. nov., holotype, ♂, habitus, RBINS (leg. C. Taylor and U. Chang; photo A. Samoh). Barcode reference JP1F.

WING (Fig. 4). Clear. Haltere white.

LEGS. Yellow, including all tarsomeres. Fore femur with a single row of short white ventral bristles, nearly half as long as femur is wide. Mid femur with a row of ventral bristles that are longest in basal half, brownish and becoming shorter towards tip. Bristles are pale brownish in basal half. Mid tibia with a row of tiny dark spine-like ventral bristles in apical half only, row ending in a tiny black apical spine. Hind tibia with a pale anterodorsal bristle near middle.

ABDOMEN. Tergites 2–3 and 6–7 yellowish (not brown). Tergite 4 long, black and covered with long pale bristles that are not squamiform. Tergite 5 very narrow, with a row of indistinct pale squamiform bristles. Terminalia (Fig. 5) brown, but hypandrium yellowish at base.

TERMINALIA. Right epandrial lamella with a forked apex, right margin with four strong bristles, left fork with short bristles, right fork almost bare (Fig. 5A). Cerci apically fused, with a few strong bristles on right side (Fig. 5B). Tip of the cercus blunt (Fig. 4D). Left surstyli with a wide truncate tip (Fig. 5C) with a small notch near apex (Fig. 5B, not visible on Fig. 5C). The apical border before the notch with pronounced papillae (not visible on Fig. 5 C due to bend of the surstyli).

Female

BODY. 1.7 mm long; wing 1.6 mm long.

Resembling male in most aspects except the mid femur with only white ventral bristles and the mid tibia without ventral spinules and lacking the tiny apical spine. Tergites 4–5 and 8 black. Cerci short, brown. Sternite 10 not pronounced.

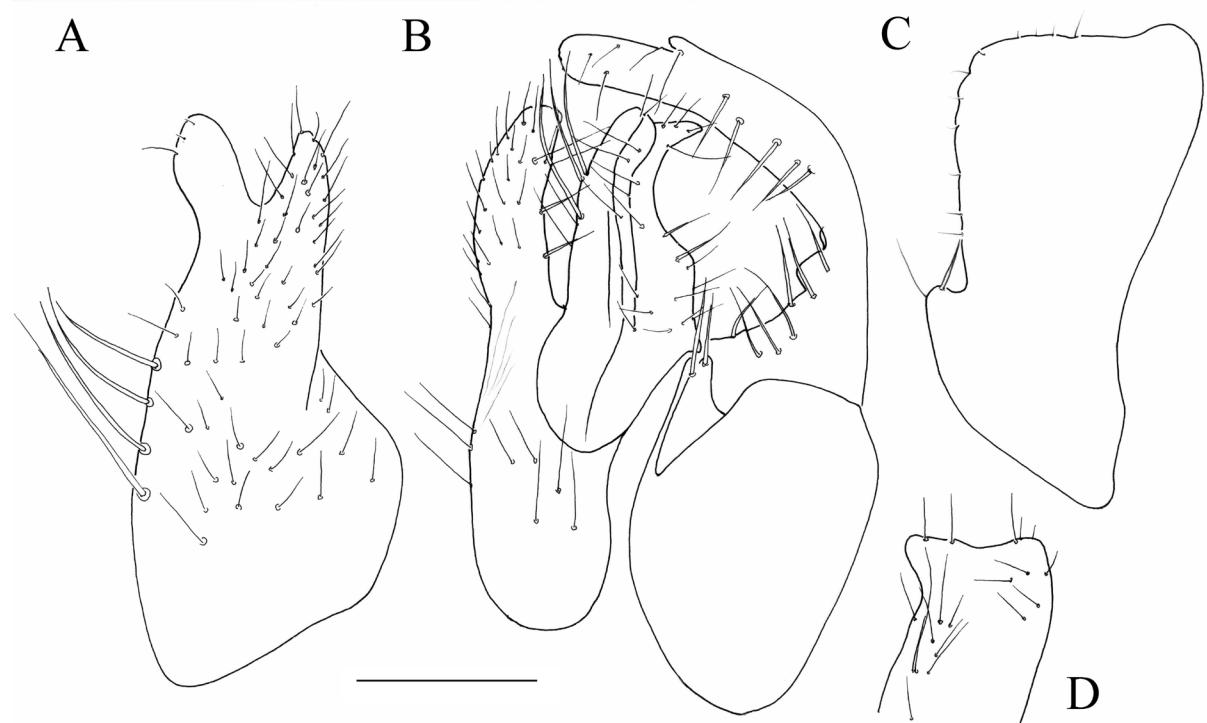


Fig. 5. *Elaphropeza furcatella* sp. nov., male terminalia, RBINS (leg. C. Taylor and U. Chang). **A.** Right epandrial lamella. **B.** Epandrium, dorsal view. **C.** Left surstyli. **D.** Tip of fused cerci. Scale bar: 0.1 mm.

Remarks

The most striking character in this species is the forked right epandrial lamella, which is quite unique in *Elaphropeza*. The acrostichal bristles do not reach the anterior border of the scutellum, but the presence of a small hair beside the most apical dorsocentrals might be confusing. The fore and mid tibiae and tarsi are pale yellowish, but sometimes in the female they are dusky yellow, which can lead to its being confused with *E. riataeae*.

Elaphropeza guenardi sp. nov.

[urn:lsid:zoobank.org:act:FC83E430-3761-4BD4-B4D9-82663F8CEFE8](https://lsid.zoobank.org/act:FC83E430-3761-4BD4-B4D9-82663F8CEFE8)

Figs 6–7

Etymology

The new species is dedicated to Prof. Benoit Guénard from Hong Kong University, who ran the entomological part of the survey of the mangroves of Hong Kong.

Material examined

Holotype

HONG KONG • ♂; Tung Chung (14M1); 22.28125° N, 113.92890° E; C. Taylor and U. Chang leg.; 18–25 Oct. 2017; dissected and drawn (Fig. 6), with barcode reference JP1A; RBINS.

Paratypes

HONG KONG • 1 ♂; same collection data as for holotype; RBINS • 1 ♂; Sam A Tsuen (5AM1); 22.51534° N, 114.27121° E; C. Taylor and U. Chang leg.; 11–27 Dec. 2017; RBINS.

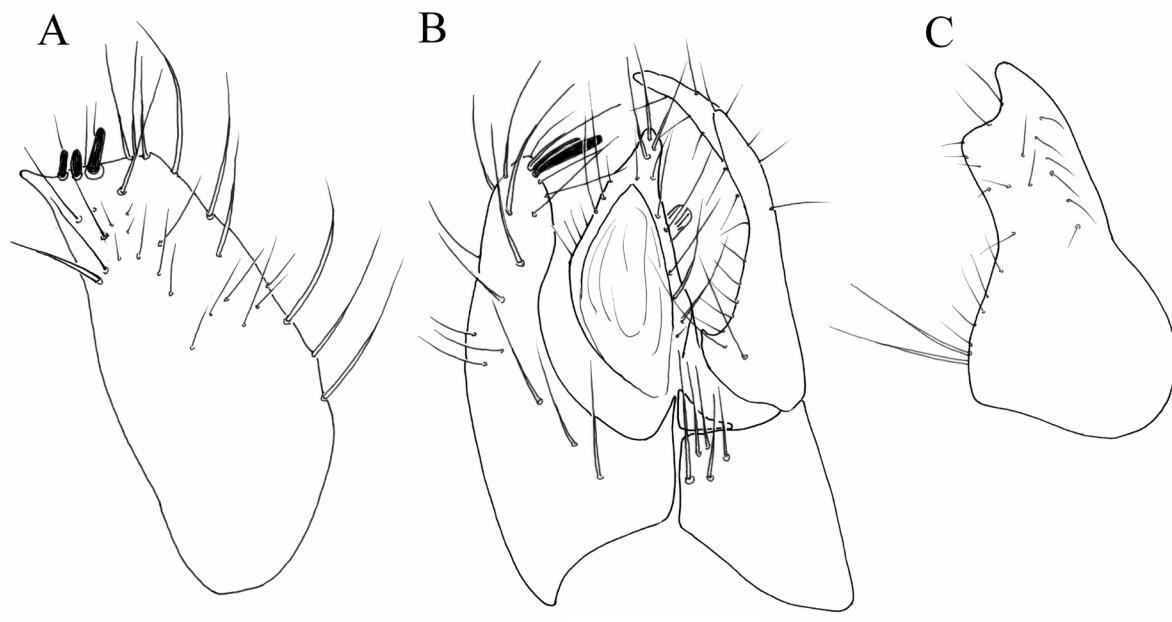


Fig. 6. *Elaphropeza guenardi* sp. nov., holotype, male terminalia (leg. C. Taylor and U. Chang; RBINS). **A.** Right epandrial lamella. **B.** Epandrium dorsal view. **C.** Left surstyli. Barcode reference JP1A. Scale bar: 0.1 mm.

Description

Male (Fig. 7)

BODY. 1.2 – 1.5 mm long; wing 1.3 mm long.

HEAD. Occiput black, a pair of long pale ocellars. A single pair of long pale verticals (outer pair indistinct). Antenna with scape and pedicel yellow, postpedicel and stylus brown. Postpedicel 4.6× as long as wide;



Fig. 7. *Elaphropeza guenardi* sp. nov., holotype, ♂, habitus, RBINS (leg. C. Taylor and U. Chang; photo A. Samoh).

stylus nearly as long as postpedicel ($0.8 \times$). Palpus rounded at base, but tip pointed, yellow with pale bristles.

THORAX. Entirely orange yellow including scutellum and metanotum. Acrostichals and dorsocentrals multiserial, acrostichals reaching the border of the scutellum. A single prescutellar dorsocentral. Two notopleurals.

LEGS. Entirely yellow, except for dusky yellow fore tibia and tarsus and tarsomere 5 of all legs. Mid femur with minute fine ventral bristles only, as well as mid tibia. Hind tibia with a pale brown anterodorsal before middle, ventrally set with long white hairs, nearly as long as tibia is wide. Hind tarsomere 1 long and a little inflated, ventrally with pale brownish bristles nearly as long as the tarsomere is wide.

WING (Fig. 7). Haltere not white, but dusky.

ABDOMEN. Tergites 2–3 light brownish, tergite 4 black, densely set with pale squamiform bristles, tergite 5 black, narrow, with a row of small squamiform bristles. Tergites and sternites 7 and 8 brown.

TERMINALIA (Fig. 6). Cerci fused at tip, fused part short, pointed, bearing a few long setae (Fig. 6B). Right epandrial lamella with truncate tip, produced into a point on right side. Apical border bearing three black tooth-like spines (Fig. 6A). Left epandrial lamella fused with hypandrium, bearing five distinct setae (Fig. 7B). Left surstyli with a pair of long setae at base and tip with a shallow indentation (Fig. 7C).

Female

Unknown.

Remarks

The new species is closely related to *E. asiophila* Shamshev & Grootaert, 2007. The differences are mainly in the male terminalia. *Elaphropeza guenardi* sp. nov. has three black, tooth-like spines on the apex of the right epandrial lamella, while there are only two spines in *E. asiophila*. The apex of the fused part of the cerci is longer in *E. asiophila* and the shape of the left surstyli and bristling is different. Moreover, the species differs in 4.5% of the barcode.

In the key of Shamshev & Grootaert (2007), *E. guenardi* sp. nov. will key out as *E. ubinensis* Shamshev & Grootaert, 2007 because the postpedicel is $4.6 \times$ as long as wide and the stylus is longer in both species than in *E. asiophila*. However, *E. ubinensis* has a brownish metanotum that is yellow in both *E. guenardi* sp. nov. and *E. asiophila*. In *E. ubinensis* the fused tip of the cerci is long and bears long strong spines.

Elaphropeza hongkongensis sp. nov.

[urn:lsid:zoobank.org:act:8FDF0480-372A-4135-A1C4-FA4551C274E5](https://lsid.zoobank.org/act:8FDF0480-372A-4135-A1C4-FA4551C274E5)

Figs 8–9

Etymology

The new species was the most abundant species during our study and it is therefore named after Hong Kong.

Material examined

Holotype

HONG KONG • ♂, Tung Chung (14M1); 22.28125° N, 113.92890° E; C. Taylor and U. Chang leg.; 18–25 Oct. 2017; dissected and figured (Figs 8–9); RBINS.

Paratypes

HONG KONG • 4 ♂♂; same collection data as for holotype; RBINS • 7 ♂♂; Sam A Chung (5AM1); 22.50829° N, 114.27248° E; C. Taylor and U. Chang leg.; 11 Nov.–27 Dec. 2017; all males with fore tibia ventrally brownish; RBINS • 1 ♂; Tung Chung (14M1); 22.28125° N, 113.92890° E; C. Taylor and U. Chang leg.; 18–25 Oct. 2017; RBINS • 1 ♂, 2 ♀♀; Tung Chung (14M2); 22.28125° N, 113.92890° E; C. Taylor and U. Chang leg.; 25 Oct.–2 Nov. 2017; with barcode references: HKC0000815 ♀, HKC0000818 ♀, HKC0000813 ♂; RBINS • 2 ♂♂, 2 ♀♀; Hang Mei (17BM1); 22.25273° N, 113.86829° E; C. Taylor and U. Chang leg.; 27 Oct.–9 Nov. 2017; 2 females with black sternite 10; RBINS • 2 ♂♂, 6 ♀♀; Tai O (17AM1); 22.24918° N, 113.86307° E; C. Taylor and U. Chang leg.; 27 Oct.–9 Nov. 2017; RBINS • 1 ♂, 1 ♀; Tai O (17AM1); 22.25790° N, 113.86360° E; C. Taylor and U. Chang leg.; 20 Oct.–2 Nov. 2017; RBINS • 1 ♂, 1 ♀; Tai O (17CM1); 22.25790° N, 113.86360° E; C. Taylor and U. Chang leg.; 20 Oct.–2 Nov. 2017; RBINS • 1 ♀; Wong Chuk Wan (34M1); 22.39563° N, 114.28617° E; C. Taylor and U. Chang leg.; 5–19 Dec. 2017; barcode reference HKC0000954; RBINS • 1 ♂, 5 ♀♀; Ho Chung (38BM1); 22.35366° N, 114.25207° E; C. Taylor and U. Chang leg.; 4 Dec. 2017; barcode references: HKC0000752 ♀, HKC0000753 ♀, HKC0000988 ♀, KC0000750 ♀, HKC0000756 ♂, HKC0000757 ♀; RBINS.

Description

Male (Fig. 8)

BODY. 1.7 mm long; wing 1.6 mm long (holotype).



Fig. 8. *Elaphropeza hongkongensis* sp. nov., holotype, ♂, habitus, RBINS (leg. C. Taylor and U. Chang; photo A. Samoh).

HEAD. Occiput black; verticals yellow, inner vertical bristle long, outer one less than half as long as inner one. Postpedicel brownish in apical part and yellow basally, nearly $3.5 \times$ as long as wide, stylus a little longer than scape, pedicel and postpedicel together.

THORAX. Yellow, but scutellum and metanotum black; acrostichals irregular tri-serial at base, becoming biserial near middle, not reaching the border of the scutellum. Only one pale brownish long prescutellar.

LEGS. Yellow with apical tarsomere of all legs black. Fore femur with a brown preapical posteroventral bristle as long as femur is wide. Mid femur with a double row of ventral spinules, anterior row shorter than posterior row. Mid tibia ventrally with a row of short, fine, spine-like bristles ending in a subapical, brown, claw-like spine; hind tibia with one strong brown anterodorsal bristle.

ABDOMEN (Fig. 8). Tergites 2–3 pale, yellowish; tergite 4 large, black with yellow hairs; tergite 5 very narrow apically, with short squamiform setae, tergites 6 and 7 yellow.

TERMINALIA (Fig. 9). Base of right epandrial lamella largely yellow, apical part yellow; cerci brown; dorsal half of surstyli yellowish brown, ventral half almost black. Cerci narrowly fused with right cercus small, left cercus very large (Fig. 9B). Left surstylus large, with a deep notch on dorsal border (Fig. 9C).

Female

BODY. 2–2.3 mm long; wing 1.6–1.7 mm long.

Similar to male. Abdominal segment 8 enlarged.

Remarks

This species is similar to *E. feminata* Shamshev & Grootaert, 2007 in most aspects. However, the notch on the dorsal side of the left surstylus is in a different position than in *E. feminata*. In the latter, it is a shallow notch on the apical border while in *E. hongkongensis* sp. nov. it is a deeper notch on the dorsal border.

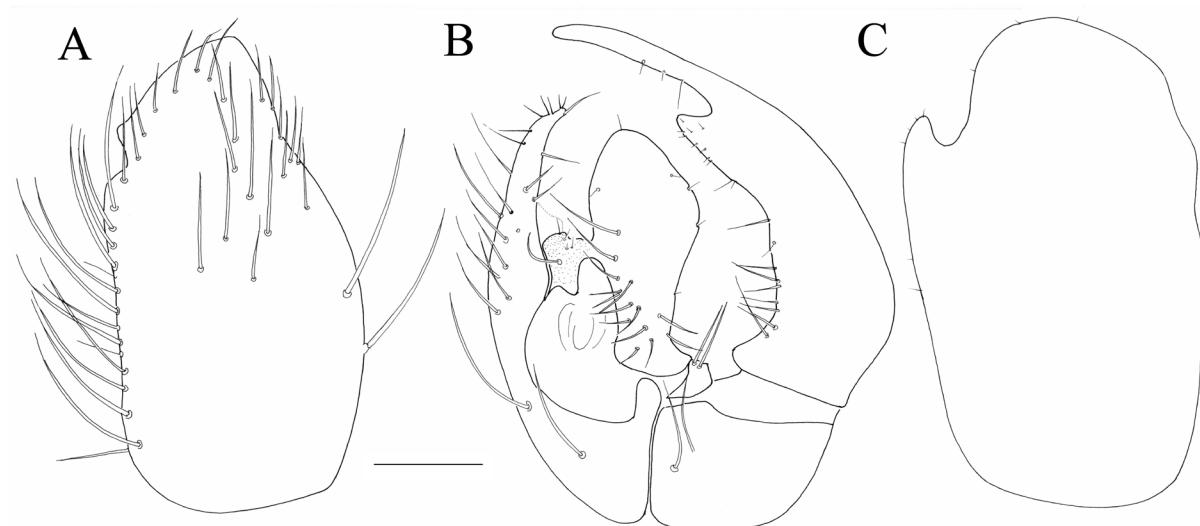


Fig. 9. *Elaphropeza hongkongensis* sp. nov., holotype, male terminalia, RBINS (leg. C. Taylor and U. Chang). **A.** Right epandrial lamella. **B.** Epandrium dorsal view. **C.** Left surstylus. Scale bar: 0.1 mm.

Elaphropeza hongshulin sp. nov.
urn:lsid:zoobank.org:act:9128B249-0D8C-4960-9E65-CE41C89BA0DC
Figs 10–11

Etymology

The new species is named in reference to the mangroves, Hong-Shu-Lin [phonetically spelled Hóng Shù Lín], meaning ‘mangrove’ in Cantonese.

Material examined

Holotype

HONG KONG • ♂; Sam A Tsuen (5AM1); 22.51534° N, 114.27121° E; Malaise trap; C. Taylor and U. Chang leg.; 11–27 Dec. 2017; barcode reference JP1D; RBINS.

Paratypes

HONG KONG • 1 ♂, 7 ♀♀; Tai Tan (28M1); 22.43857° N, 114.33327° E; C. Taylor and U. Chang leg.; 5–19 Dec. 2017; 1 female with barcode reference JP2G; RBINS • 1 ♂; Sam A Chung (5BM1), sandy back mangrove near a stream; 22.50829° N, 114.27248° E; C. Taylor and U. Chang leg.; 11–27 Dec. 2017; RBINS • 1 ♂; Tai Tam (22M1); 22.24614° N, 114.22334° E; C. Taylor and U. Chang leg.; 9–23 Oct. 2017; barcode reference HKC_0000792; RBINS • 1 ♂; Tung Chung (14M2), sandy back mangrove; 22.28125° N, 113.9289° E; C. Taylor and U. Chang leg.; 25–31 Oct. 2017; barcode reference HKC_0000819; RBINS • 1 ♀; Ho Chung (Nam Wai) (38AM1), muddy back mangrove; 22.35347° N, 114.25622° E; C. Taylor and U. Chang leg.; 4–18 Dec. 2017; barcode reference HKC_0000194; RBINS.

Description

Male (Fig. 10)

BODY. 2.3–2.4 mm long; wing 2.3–2.4 mm long.

HEAD. Occiput black, postpedicel 3.0× as long as wide, stylus nearly 2.0× as long as postpedicel; scape and pedicel yellow, postpedicel pale brownish.

THORAX. Yellow, including scutellum and pleura; metanotum brown. Acrostichals biserial (tri-serial in front), lacking on prescutellar depression; dorsocentrals 1–2-serial.

LEGS. Yellow, including fore tibia; tarsomere 5 of all legs brownish black. Mid tibia with a tiny black apical spine. Hind tibia with one pale anterodorsal bristle.

WING. Clear without colour pattern. Haltere white.

ABDOMEN. Yellow except for the large black tergite 4, which bears only fine pale setae; tergite 5 brown, very narrow, with a single row of indistinct squamiform setae.

TERMINALIA (Fig. 11A–D). Right epandrial lamella brownish on apical half, yellow on basal half, not truncate, with ordinary apical setae and thus lacking the three black spines on the apical border as in *E. malaysensis* (Fig. 11E), but with a single black subapical spine (Fig. 11B). Left surstyli large, brown. Cerci apically fused, yellow, with large extensions on apex (see *E. malaysensis*).

Female

BODY. 2.4 mm long; wing 2.3–2.4 mm long.

Similar to male.

Remarks

Elaphropeza hongshulin sp. nov. belongs to a complex of seven species, the others being: *E. chanae* Grootaert & Shamshev, 2012, *E. chanoides* Grootaert & Shamshev, 2015, *E. gohae* Grootaert & Shamshev, 2012, *E. lowi* Grootaert & Shamshev, 2012, *E. lowioides* Grootaert & Shamshev, 2015 and *E. malayensis* Shamshev & Grootaert, 2007. Externally, they are difficult to distinguish, and the male genitalia should be checked if possible. The barcodes suggest that the new species is closer related to *E. lowi* than to *E. malayensis*.

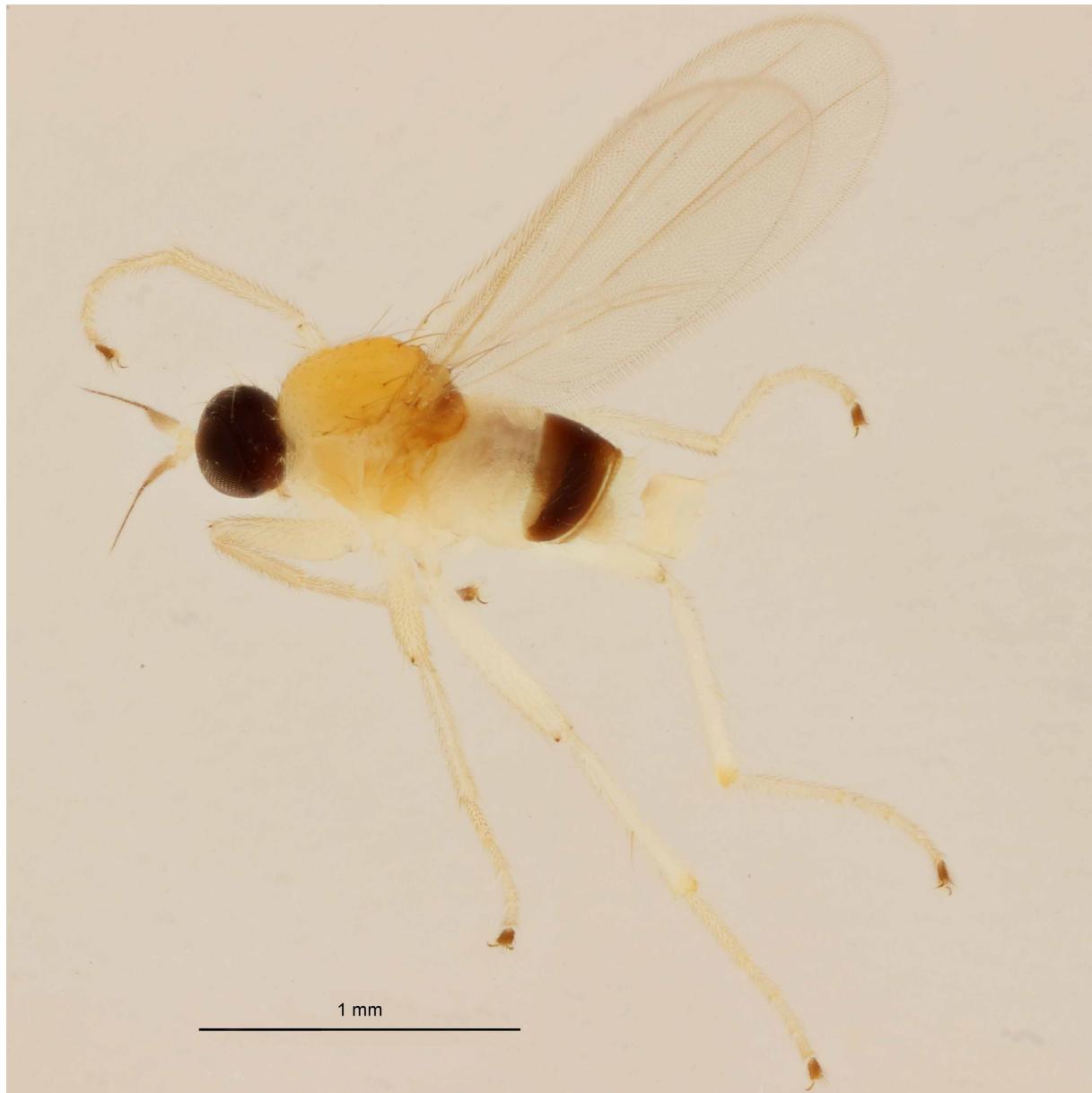


Fig. 10. *Elaphropeza hongshulin* sp. nov., holotype, ♂, habitus, RBINS (leg. C. Taylor and U. Chang; photo A. Samoh).

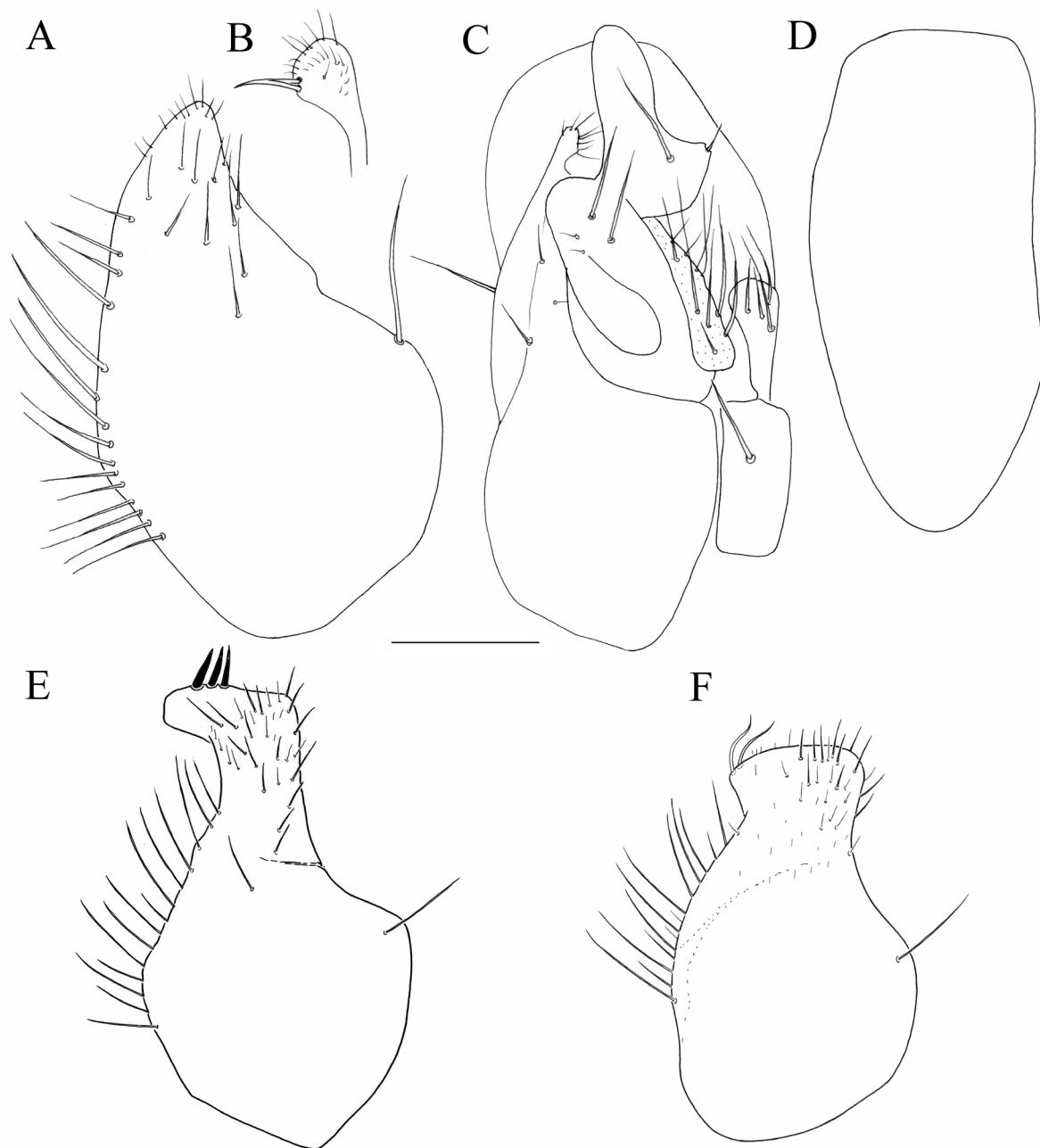


Fig. 11. A–D. *Elaphropeza hongshulin* sp. nov., holotype, RBINS (leg. C. Taylor and U. Chang). A. Right epandrial lamella. B. Tip of right surstylius, lateral view. C. Epandrium dorsal view. D. Left surstylius. — E. *E. malayensis* Shamshev & Grootaert, 2007, right epandrial lamella (after Grootaert & Shamshev 2012). — F. *E. lowi* Grootaert & Shamshev, 2012, right epandrial lamella (after Grootaert & Shamshev 2012). Scale bar: 0.1 mm.

Elaphropeza riatanae Shamshev & Grootaert, 2007
Figs 12–13

Elaphropeza riatanae Shamshev & Grootaert, 2007: 88, figs 141–144; (type locality: Pulau Ubin, Chek Jawa, Singapore).

Elaphropeza riatanae – Grootaert & Shamshev 2012: 88, new records.

Material examined

HONG KONG • 1 ♂; Tai Tan (28M1); 22.43857° N, 114.33327° E; C. Taylor and U. Chang leg.; 5–19 Dec. 2017; male genitalia as in holotype but fore tibiae not brown, tarsus brown; RBINS • 2 ♂♂; Sam A Chung (5BM1); 22.50829° N, 114.27248° E; C. Taylor and U. Chang leg.; 11–27 Dec. 2017; 1 male has fore tibia and tarsus brown, mid tarsus as well; scutellum with only the margins brown while the second male has a black scutellum; RBINS • 3 ♂♂; Sam A Tsuen (5AM1); 22.51534° N, 114.27121° E; C. Taylor and U. Chang leg.; 11–27 Dec. 2017; RBINS • 1 ♂; Tai Tan (28M1); 22.43857° N, 114.33327° E; C. Taylor and U. Chang leg.; 5–19 Dec. 2017; RBINS • 1 ♂; Yim Tin Tsai (45AM1); 22.37576° N, 114.30160° E; C. Taylor and U. Chang leg.; 24 Nov. 2017; RBINS • 5 ♂♂, 1 ♀; Tai O (17CM1); 22.25790° N, 113.86360° E; C. Taylor and U. Chang leg.; 20 Oct.–2 Nov. 2017; RBINS • 3 ♂♂, 1 ♀; Wong Chuk Wan (34M1); 22.39563° N, 114.28617° E; 5–19 Dec. 2017; muddy back mangrove; barcode references: HKC0000952 ♀, HKC0000956 ♂, HKC0000958 ♂, HKC0000960 ♂; RBINS • 1 ♂; Shui Hau (19M1);



Fig. 12. *Elaphropeza riatanae* Shamshev & Grootaert, 2007, ♂, habitus, RBINS (leg. C. Taylor and U. Chang; photo A. Samoh).

22.21936°N, 113.91898°E; 1–14 Nov. 2017; sandy back mangrove; male terminalia figured (Fig. 13); barcode reference JP1E; RBINS • 1 ♂; Sam A Chung (5BM1); 22.50829°N, 114.27248°E; C. Taylor and U. Chang leg.; 11–27 Dec. 2017; barcode reference JP1H; RBINS • 1 ♀; Ho Chung (38BM1); 22.35366°N, 114.25207°E; 4–18 Dec. 2017; muddy back mangrove; this female has a yellow scutellum; RBINS • 1 ♂; same collection data as for preceding; barcode reference HKC0000751; RBINS • 1 ♀; same collection data as for preceding; with black scutellum and the other dark body parts are also darker, fore tibia and tarsus, brownish patch on postalar callus, haltere dusky; barcode reference HKC0000747; RBINS • 1 ♂; Tai Tam (22M1); 22.24614°N, 114.22334°E; 9–23 Oct. 2017; sandy back mangrove; barcode reference HKC0000786; RBINS • 1 ♂; Sheung Pak Nai (10M1); 22.45197°N, 113.96253°E; 15 Nov.–1 Dec. 2017; sandy back mangrove; barcode reference HKC0001044; RBINS.

Description

Male (Fig. 12)

BODY. 1.5–1.6 mm long; wing 1.4–1.5 mm long.

HEAD. Occiput black, all setae pale yellow. Scape yellow, apical half of pedicel yellowish brown, postpedicel brown, but a little paler at base; postpedicel nearly 5.0× as long as wide, stylus about as long as postpedicel. Ocellar bristles a little shorter than the verticals.

THORAX. Scutum orange yellow, scutellum brown and metanotum black; acrostichal and dorsocentral bristles multiserial, reaching the scutellum.

LEGS. Yellow with brownish pattern; fore tibia and tarsus and mid tarsus yellowish brown, in contrast to yellow femora. Mid tibia with brown ventral spinules in apical half, no apical spine. Hind tibia with one anterodorsal bristle near middle; tarsomere 1 yellow, with an irregular double row of brown spinules about as long as tarsomere is wide.

ABDOMEN. Tergites 2 and 3 brown at side, tergites 4 and 5 black, with squamiform setae, tergites 6 and 7 entirely black.

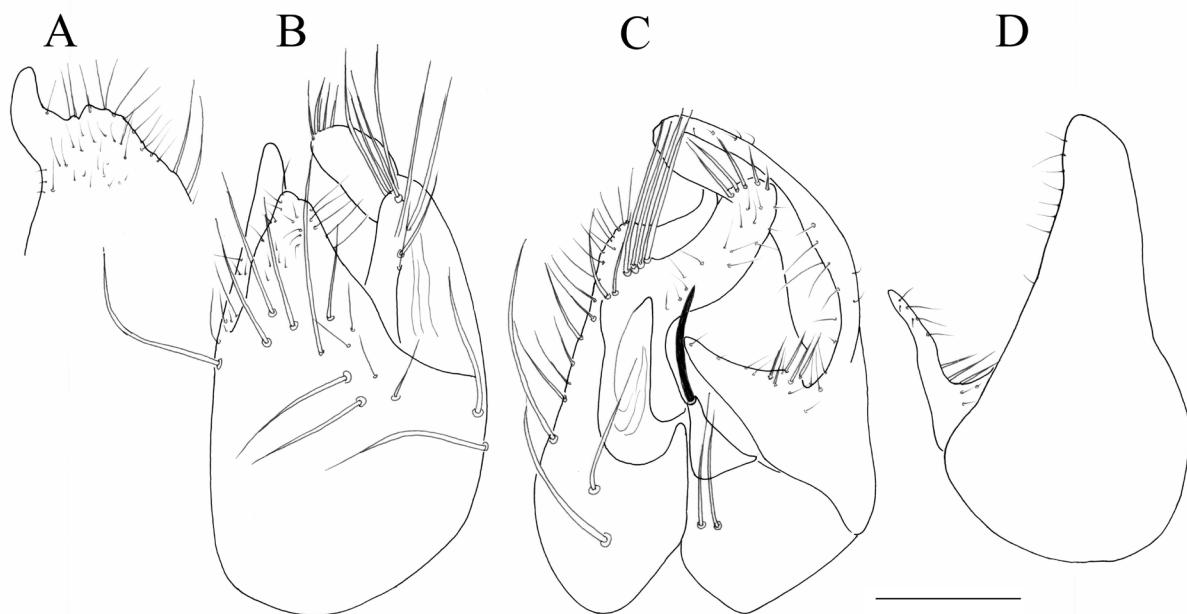


Fig. 13. *Elaphropeza riatanae* Shamshev & Grootaert, 2007, male terminalia (19M1), RBINS (leg. C. Taylor and U. Chang). **A.** Tip of right epandrial lamella. **B.** Right epandrial lamella. **C.** Epandrium dorsal view. **D.** Left surstyli. Scale bar: 0.1 mm.

TERMINALIA (Fig. 13). Black. Right epandrial lamella subtriangular (Fig. 13B), tip bent and elongate to right side (Fig. 13A). Cerci fused with a row of long bristles at base of fused part, tip elongate and bent to left, with a few short bristles apically. Left epandrial lamella fused with hypandrium, bearing a papilla-like protuberance bearing a strong black bristle, with two long bristles at tip of hypandrium (Fig. 13C). Left surstyli triangular in lateral view (Fig. 13D), with a long protuberance at base elongate to right side and bearing there a few short, strong bristles.

Female

BODY. 1.5–1.6 mm long; wing 1.4–1.7 mm long.

Legs with identical colour pattern as in male. Ventral spinules on mid tibia less distinct than in male. Tergite 4 shorter than in male, with finer squamiform setae.

Remarks

The male terminalia of the Hong Kong specimens are similar to those of specimens from Singapore, though there are differences. The tip of the fused part of the cerci in Hong Kong males is more bent to the left and bearing at its tip a few short bristles. There are hardly any bent or short bristles on the tip of the cercus in the Singaporean specimens. The tip of the left surstyli in Hong Kong specimens seems to be more pointed than in the Singaporean specimens. Since there are no barcodes available for the Singaporean specimens to indicate that this variation is related to a large genetic distance, the specimens are considered conspecific. *Elaphropeza riatanae* is rare in Singapore, while very common in Hong Kong.

In the key to the Oriental species (Grootaert & Shamshev 2012) of *Elaphropeza* it is stated that the scutellum is brown in this species. However, in Hong Kong there is a large variation in colour of the scutellum, from specimens with completely yellow scutellum, though generally the margin of the scutellum with the scutum is brown. Some specimens have the central area of the scutellum brown, while in others the scutellum is entirely black. The barcodes of these colour variations form a cluster of less than 1%. Thus, it is considered that all form a single species. Moreover, the populations are mixed. Specimens that are overall darker, with darker fore tibia and tarsus, generally have a darker scutellum.

Elaphropeza xanthocephala Bezzi, 1912

Figs 14–15

Elaphropeza xanthocephala Bezzi, 1912: 488 (type locality: Taiwan, Takao (currently Kaohsiung)).

Diagnosis

A yellow species with a yellow occiput and a yellow scutum, but a black scutellum and metanotum. Metapleuron yellow. The tip of the hypopleuron (meron) above hind coxae with a black spot.

Material examined

HONG KONG • 1 ♂; Wong Chuk Wan (34M1); 22.39563° N, 114.28617° E; C. Taylor and U. Chang leg.; 5–19 Dec. 2017; Malaise trap in back mangrove; barcode reference HKC0000951; RBINS.

Description

Male (Fig. 14)

HEAD. A pair of long, somewhat dark vertical setae. Antenna long. Scape yellow, pedicel dusky yellow, postpedicel entirely brown, but base yellowish brown, stylus brown. Ratio: 0.03 : 0.05 : 0.022 : 0.325.

Postpedicel is $4.25 \times$ as long as wide. Stylus is $1.4 \times$ as long as postpedicel. Palpus yellow, elongate and bearing a few long setae.

THORAX. Yellow, but metanotum black and metapleuron entirely yellow.

LEGS. Yellow including all coxae. Tip of hind femur dusky. All tarsomeres 5 brown. Apex of hind tibia brown. Spur pronounced.

FORE LEG. Femur lacking ventral setae. Tibia with some longer setulae.

MID LEG. Femur ventrally with a double row of spinules, multiserial at extreme base. Apical half of tibia somewhat inflated, ventrally bearing long, flattened setulae.

HIND LEG. Femur swollen in apical half, narrow in basal half; ventrally with a single row of short brown setae. Tibia with a long brown anterodorsal seta near middle. Apex with a rather strong apical rounded spur. Tarsomere 1 with a strong anteroventral seta before middle.

WING. Haltere brown.

ABDOMEN. Tergites 2–3 white above, brownish at sides. Tergite 4 large, with brown squamiform setae. Tergite 5 narrow, brown above, yellowish at side. Tergites 6 and 7 yellow.



Fig. 14. *Elaphropeza xanthocephala* Bezzi, 1912, ♂, habitus, RBINS (leg. C. Taylor and U. Chang; photo C. Locatelli).

TERMINALIA. Pale brown (Fig. 15). Right epandrial lamella bearing two strong, flattened brown setae (Fig. 15A).

Female

Unknown.

Remarks

Elaphropeza xanthocephala is the single species with a yellow occiput occurring in Hong Kong mangroves and hence easy to recognize.

In his description, Bezzi (1912) writes that the metapleura is shining black and in the diagnosis that the metanotum is black. In our specimen the metapleura is entirely yellow and the metanotum is black. We suspect this is a lapsus or that Bezzi referred to the hypopleuron, which has an apical black spot.

Bezzi (1912) had only a single specimen from Takao which is located at the coast and it is not unlikely that this specimen was collected in the mangrove of Takao.

Discussion

The present study is based on a small sample of 105 specimens of *Elaphropeza* collected in 14 mangrove sites all around Hong Kong during autumn 2017 (Fig. 1). Seven different morpho-species were found that were congruent with the COI barcodes that were obtained for all seven species.

Three species were known before: *Elaphropeza riatanae* described from Singapore, and *E. calcarifera* and *E. xanthocephala*, both from Taiwan. The species turnover between the southern part of the South China Sea, in casu Singapore with Hong Kong in the northern part of the South China Sea, is high.

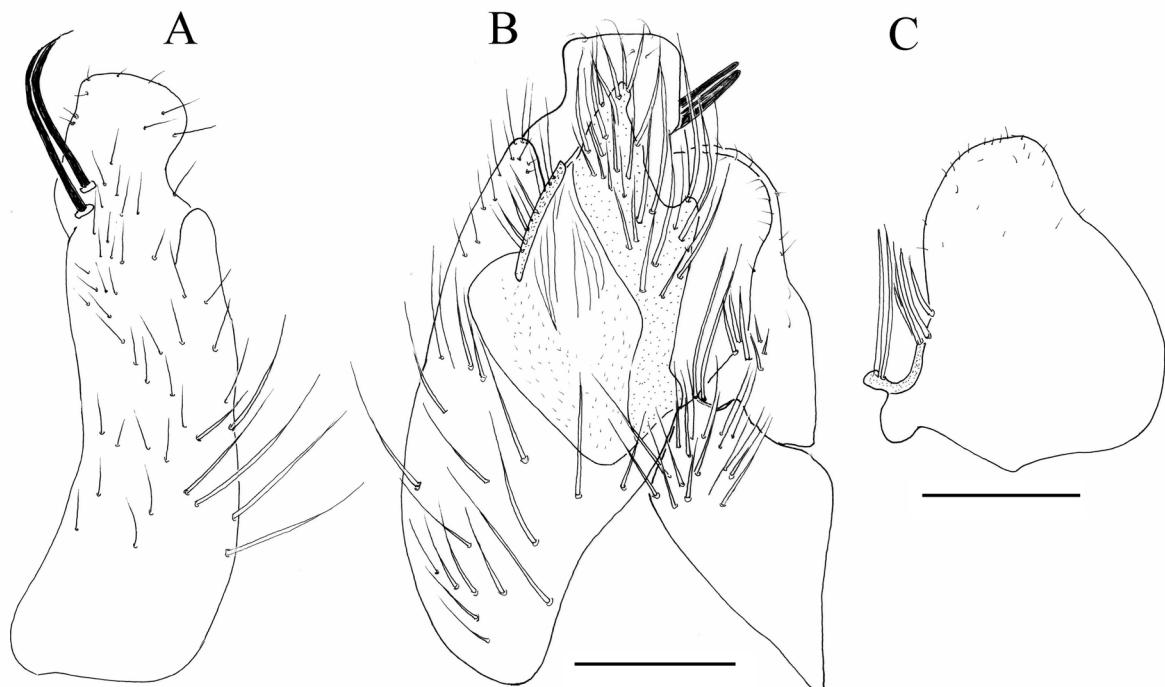


Fig. 15. *Elaphropeza xanthocephala* Bezzi, 1912, male terminalia, RBINS (leg. C. Taylor and U. Chang). **A.** Right epandrial lamella. **B.** Epandrium, dorsal view. **C.** Left surstylius. Scale bars: 0.1 mm.

Only *E. riatanae* is found in both regions. Unfortunately, no molecular data are available for *E. riatanae* from Singapore, so that the genetic distance with *E. riatanae* from Hong Kong remains unknown. This species is not common in Singapore, while it seems to be one of the dominant species in Hong Kong mangroves.

Four species are new for science. These four morpho-species are morphologically closely related to species known from Singapore. *Elaphropeza furcatella* sp. nov. forms a clade with *E. furca* Shamshev & Grootaert, 2007 and *E. riatanae* Shamshev & Grootaert, 2007; *E. guenardi* sp. nov. is a sibling species of *E. asiophila* Shamshev & Grootaert, 2007; *E. hongkongensis* sp. nov. is very closely related to *E. feminata* Shamshev & Grootaert, 2007 and *E. hongshulin* sp. nov. resembles *E. lowi* Grootaert & Shamshev, 2012. This relationship is more or less reflected in the Maximum Composite Likelihood model (Fig. 16), though there is no real support for the relationship since the bootstrap values are very low. The highest bootstrap value, which is only 74, connects *E. guenardi* with *E. asiophila*. Since the bootstraps are very low, as can be seen in Fig. 16, it is clear that the COI barcodes cannot be used in this sample of *Elaphropeza* to do a phylogeny of the genus or even of the species from mangroves alone. Apparently, speciation took place a long time ago.

Over the last 2 million years, glaciations caused a sea level drop more than 50 times. The southern third of the South China Sea was dry, so that the mangroves from the south following the sea border came much closer to the mangroves in Hong Kong (Voris 2000; Grootaert 2009).

Up to now, 67 species of *Elaphropeza* have been reported from Singapore (Shamshev & Grootaert 2007; Grootaert & Shamshev 2012, 2015) and 49 species were recorded in mangrove. Ten species were found in front mangroves while 39 species occurred in back mangroves. In fact, 29 species are found exclusively in mangroves while the others also occur in terrestrial habitats such as beach forest, swamp forest or even old growth forest. Except for the black *E. obscura* Grootaert & Shamshev, 2015, all other species of the front mangrove are entirely yellow. This is remarkable, since the front mangrove is the part exposed to the sun and generally hybotid species occurring in sun-exposed habitats are entirely black, while species occurring in shaded areas are yellow. Moreover, some of these yellow species from the front mangrove have also been seen foraging on rocky shores completely exposed to the sun (Grootaert unpublished).

Only seven species of *Elaphropeza* are found in the mangroves of Hong Kong and there may be several reasons for this low diversity. First of all, the sampling effort is low compared to that in Singapore (Grootaert & Shamshev 2012, 2015), so that in the future the number of species might prove to be higher in Hong Kong. Secondly, *Elaphropeza* thrives in tropical regions and that is also why fewer species are found in Hong Kong, since it is situated at a much higher latitude and has a rather Mediterranean climate with Palaearctic relics. The hybotid *Syndyas nigripes* (Zetterstedt, 1842), a boreal Palaearctic species, is such an example (Grootaert, unpublished).

It is remarkable that five of the seven species found in the mangroves of Hong Kong are almost identical to species described from Singapore. They all belong to a species group with entirely yellow scutum and similar male terminalia. This indicates that a whole species group adapted to marine conditions. At least, this is the situation for Hong Kong, while more species lineages adapted to mangrove conditions in Singapore. At present, none of the *Elaphropeza* from mainland China, in particular nearby Guangdong, have been reported in the mangroves of Hong Kong (Yang *et al.* 2006).

Acknowledgements

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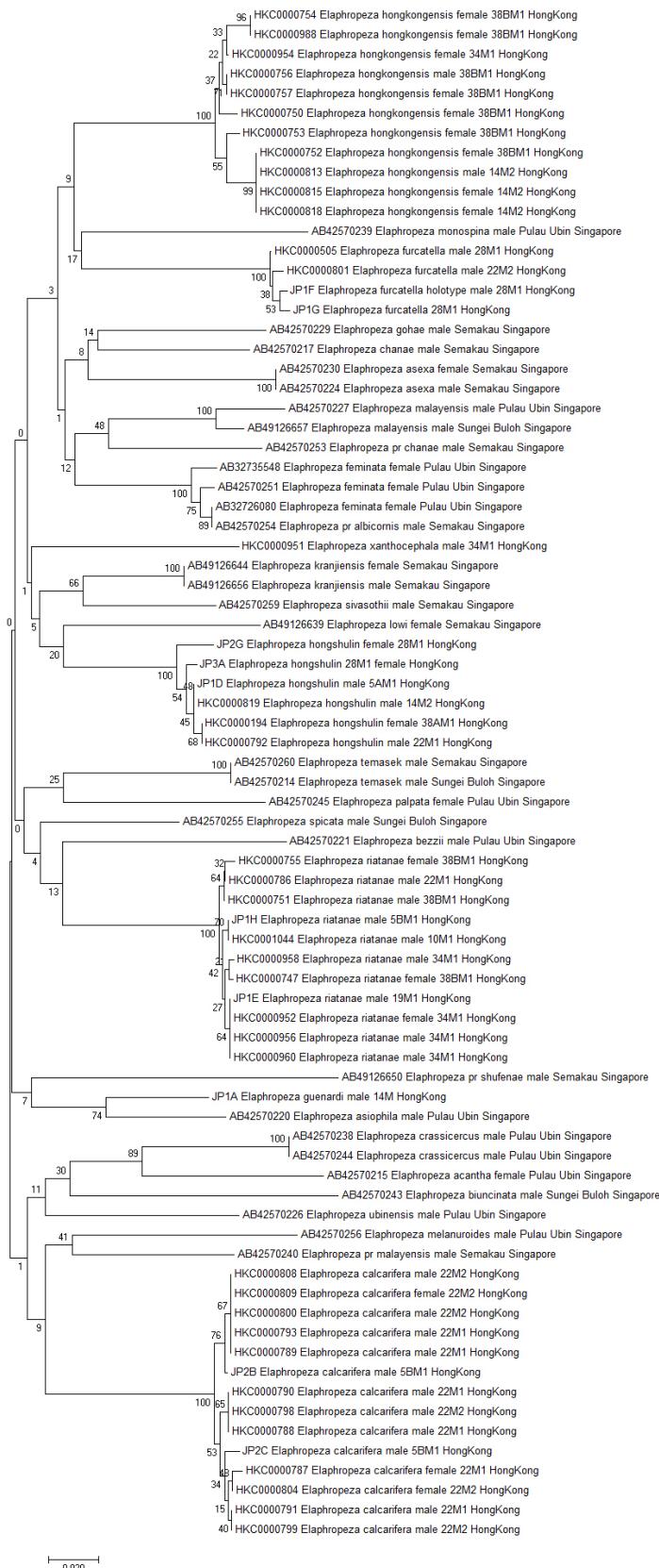


Fig. 16. Maximum Composite Likelihood model for 29 species of *Elaphropeza* based on COI barcodes from specimens from Singapore and Hong Kong.

University for leading the survey of the mangroves in Hong Kong and allowing me to study the Diptera of these samples. Samples were taken by Christopher Taylor and Ukyoung Chang. Stacked photos were made by Dr Abdullah Samoh and Ms Camille Locatelli. Barcoding was done by Mr Gontran Sonet (RBINS) and Ms Jayanthi Puniamoorthy (National University of Singapore). Prof. Rudolf Meier (NUS) stimulated the molecular part of the study and provided working facilities. Dr Igor Shamshev and Dr Isabella Van de Velde gave important comments on the manuscript.

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