

The *Stegana undulata* species group (Diptera: Drosophilidae) from the Oriental Region, with molecular phylogenetic analysis of the Chinese species

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Key words. Drosophilidae, systematics, molecular phylogeny, mitochondrial DNA, Oriental Region, *Stegana undulata* group, *Steganina*

Abstract. The *Stegana undulata* species group is revised and eight new species described: *S. (Steganina) flaviclypeata* Chen & Chen, sp. n., *S. (S.) flavipalpata* Chen & Chen, sp. n., *S. (S.) leucothorax* Chen & Chen, sp. n., *S. (S.) melanocheilota* Chen & Chen, sp. n. and *S. (S.) melanothorax* Chen & Chen, sp. n. from southern China, and *S. (S.) flaviscutellata* Chen & Chen, sp. n., *S. (S.) nigriclypeata* Chen & Chen, sp. n. and *S. (S.) nigripalpata* Chen & Chen, sp. n. from eastern Malaysia. A key to all the species examined based on morphological data is provided. Based on DNA sequence data of the mitochondrial *ND2* and *COI* genes, the relationship among six Chinese species of the *undulata* group and that of the *S. coleoprata* and *S. nigrolimbata* species groups of the same subgenus is investigated, using *S. emeiensis* of the subgenus *Stegana* s. str. as an out-group.

INTRODUCTION

The subgenus *Steganina* Wheeler, 1960 with 113 known species is the biggest subgenus in the genus *Stegana* Meigen, 1830. Eighty-three species of this subgenus are known from eastern and southeastern Asia (Brake & Bächli, 2008; Cao & Chen, 2008; Chen & Chen, 2008, 2009a, b; Chen et al., 2009; Cheng et al., 2009). The phylogenetic relationships of this subgenus have been analyzed (Okada, 1971; Okada & Sidorenko, 1992; Sidorenko, 2002; Otranto et al., 2008) and although more than 50 species are still ungrouped, the others have been assigned to five species groups: (1) the *coleoprata* group (Laštovka & Máca, 1982); (2) the *nigrolimbata* group, or “group 3” in Okada (1971) (Sidorenko, 2002; Cao & Chen, 2008); (3) the *ornatipes* group (Cheng et al., 2009); (4) the *shirozui* group (Chen et al., 2009) and (5) the *undulata* group, or Okada’s (1971) “group 2”, with the exclusion of two species, *S. nigrifrons* de Meijere, 1911 and *S. scutellata* de Meijere, 1911, and thus, according to Sidorenko (2002), based only on morphological characters of the nominotypical species. This species group is identified based on a combination of the following four characters: (1) face broadened ventrally with conspicuous black band below; (2) 7–13 interfrontal setulae; (3) postpronotal lobe with 2 setae; and (4) hypandrium with 1 pair of paramedian setae (Sidorenko, 2002).

In the present study, eight new species found in South China and East Malaysia are added to the *undulata* group and the relationships of the *undulata* group based on DNA sequences of the mitochondrial *ND2* and *COI* genes investigated.

MATERIAL AND METHODS

Location of type material and morphological terminology

All the type material was collected on tree trunks or tussocks along streams in forests. The specimens are deposited in the following institutions: Institute for Tropical Biology and Conservation, University Malaysia Sabah, Kota Kinabalu, Sabah, Malaysia (ITBC); Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, China (KIZ); Museum of Kinabalu Park, Sabah Parks, Sabah, Malaysia (KPSP); Museum Zoologicum Bogoriense, Bogor, Indonesia (MZB); Department of Entomology, South China Agricultural University, Guangzhou, China (SCAU); Department of Systematic Entomology, Hokkaido University Museum, Sapporo, Japan (SEHU). The morphological terminology follows McAlpine (1981) and the definitions of measurements, indices and abbreviations, Zhang & Toda (1992) and Chen & Toda (2001). H.W. Chen and X.P. Chen described the new species.

Taxa used in the phylogenetic analysis

Samples of some species of the *undulata* group, except for those from Malaysia (which had been preserved in Kahle’s solution for too long to obtain DNA), were used for DNA sequencing and phylogenetic analysis (Table 1). To test the monophyly of this group, three species, *S. nigrolimbata* Duda, 1924 (*nigrolimbata* species group), *S. pililobosa* Chen & Chen, 2008 and *S. psilolobosa* Chen & Chen, 2008 (both belonging to *coleoprata* species group) of the same subgenus *Steganina*, were included as ingroup taxa. *Stegana (Stegana) emeiensis* Sidorenko, 1997 was used as the outgroup in the phylogenetic analysis.

DNA extraction, PCR and sequencing

Total DNA was extracted from a single male using the TIAN-GEN™ DNA extraction kit following the recommended protocol. The *ND2* and *COI* fragments were amplified using the cycle protocol of Zhao et al. (2009). The PCR/sequencing primer pair for the *ND2* fragment was 5’-AAGCTACTGGGTTTCATACC-3’

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TABLE 1. Details of the samples used in the DNA sequencing and accession numbers of the *ND2* and *COI* sequences; sequences marked with asterisks are those of Li et al. (2010).

Subgenera	Species group	Species	Geographical origin	Accession numbers	
				<i>ND2</i>	<i>COI</i>
<i>Stegana</i>		<i>emeiensis</i>	Menglun, Yunnan, China	EU805515*	HM636455
<i>Steganina</i>	<i>coleoptrata</i>	<i>pililobosa</i>	Shennongjia, Hubei, China	GQ249186	HM636456
		<i>psilobosa</i>	Shennongjia, Hubei, China	GQ249187	HM636457
		<i>nigrolimbata</i>	Guangzhou, Guangdong, China	EU805513*	HM636458
	<i>undulata</i>	<i>nigrolimbata</i>	Guangzhou, Guangdong, China	EU805513*	HM636458
		<i>melanocheilota</i>	Menglun, Yunnan, China	GQ249188	HM636459
		<i>flavipalpata</i>	Nanjian, Yunnan, China	GQ249189	HM636460
		<i>flavipalpata</i>	Kunming, Yunnan, China	GQ249190	HM636461
		<i>leucothorax</i>	Menglun, Yunnan, China	GQ249191	HM636462
		<i>flaviclypeata</i>	Moxi, Sichuan, China	GQ249192	HM636463
		<i>flaviclypeata</i>	Jingdong, Yunnan, China	GQ249193	HM636464
		<i>melanothorax</i>	Menglun, Yunnan, China	GQ249194	HM636465
		<i>undulata</i>	Jianfengling, Hainan, China	GQ249195	—
		<i>undulata</i>	Mengla, Yunnan, China	GQ249196	HM636466

(Park, 1999) and 5'-AGGCGATAGATTGTAAATC-3' (He et al., 2009); the PCR/sequencing primer pair for the *COI* fragment was 5'-CGCCTAAACTTCAGCCACTT-3' (Wang et al., 2006) and 5'-CCTAAATTAGCTCATGTAGAC-3' (He et al., 2009) for *S. emeiensis* and *S. nigrolimbata*, and 5'-GGTCAACAAATCATAAAGATATTGG-3' and 5'-TAAACTTCAGGGTGA CCAAAAAATCA-3' (Folmer et al., 1994) for the other species. The PCR products were purified and then directly sequenced on an ABI3730 sequencer.

Sequence aligning and characterization

The GenBank accession numbers of the sequences used in the present analysis are shown in Table 1. The *ND2* sequences of two species, *S. emeiensis* and *S. nigrolimbata*, were obtained from GenBank. The *ND2* and *COI* sequences (Table 1) were aligned using the ClustalW method (Thompson et al., 1994) and the alignments edited manually to make it conform to the codon assignments. The alignments of the two genes were then combined for phylogenetic analyses, with the unavailable *COI* sequences for *S. undulata*-HN treated as missing data. Before the phylogenetic analysis, the sequence data were subjected to the base compositional homogeneity test using STATIO (Rzhetsky & Nei, 1995). The program DAMBE (Xia & Xie, 2001) was also used to test whether the observed index of substitution saturation (*I_{ss}*) is significantly lower than the critical index of substitution saturation (*I_{ss.c}*) (Xia et al., 2003). Models of nucleotide substitution were selected using Modeltest 3.7 (Posada & Crandall, 1998) for the whole concatenated sequences and partitioned data sets: two data sets partitioned by gene locus (*ND2* and *COI*) and six partitioned by gene locus plus codon position (1st, 2nd and 3rd).

Phylogenetic analysis

Phylogenetic trees were constructed using the Minimum Evolution (ME) method, program MEGA version 4 (Tamura et al., 2007) and concatenated sequences of the *ND2* and *COI* genes. Based on the result of model selection and the test of base compositional homogeneity using STATIO (Table 2), the Maximum Composite Likelihood model was adopted, with substitution rates across sites set as gamma distributed (shape parameter = 1.1771) and nucleotide frequencies among species set as heterogeneous. Bayesian analyses using MrBayes version 3.12 (Ronquist & Huelsenbeck, 2003) and concatenated sequences were also conducted. For the Bayesian analysis, specific nucleotide substitution models were assigned to data sets partitioned by gene locus only (2 data partitions) or by locus and codon position (6 data partitions) according to the results of model selec-

tion in Modeltest (Table 2). Two MCMC runs of 1,000,000 generations were conducted in each Bayesian analysis, with a sampling frequency of every 100 generations, and a burning-in of 2,500 early-phase samples for each run. Then a majority-rule tree showing all the compatible partitions was obtained by summarizing the remaining 15,002 samples.

SYSTEMATIC ACCOUNT

Subgenus *Steganina* Wheeler, 1960

Stegana (*Steganina*) Wheeler, 1960: 110.

Type species: *Musca coleoptrata* Scopoli, 1763.

Diagnosis. Largest diameter of eye oblique to the body axis; face with black band.

Stegana undulata species group

Diagnosis (modified from Sidorenko, 2002)

Surstylus not strongly arcuate, mostly with 1 small acute prensiseta submedially on inner margin (absent in *S. flaviscutellata* Chen & Chen, sp. n.), only distally with dense setae (Figs 4, 9, 13, 18, 22, 27, 32, 41); 10th sternite expanded to lobate distally (Figs 5, 10, 14, 19, 23, 28, 33, 42).

Description (male and female)

Head: Eyes red. Ocellar triangle black, with a pair of small setae above ocellar setae. Post-vertical setae slightly behind vertex ridge. Frons and face rectangular in lateral view. Frons shiny, with a black band and sporadic, minute setulae below (above ptilinal fissure). Proclinate orbital setae nearer to ptilinal fissure than to inner vertical setae. Face broadened ventrally; facial carina absent. Palpus with 4–5 long setae distally and several shorter setae basally. Gena broad ($ch/o \geq 0.15$), whitish yellow. Vibrissa prominent; other orals small. Occiput glossy, yellow, black around occipital foramen.

Thorax: Scutum usually with a few patches and stripes. Mesopleuron with a black longitudinal stripe above (running from propleuron to base of haltere). Postpronotal lobe with 1–3 long and a few small setae. Acrostichal setulae in approximately 10 irregular rows. Prescutellar setae 1 pair. Basal scutellar setae divergent; apical scutellars cruciate.

TABLE 2. Results of model selection, composition homogeneity test and test of substitution saturation.

	ND2				COI				ND2 + COI			
	1st-CP ^a	2nd-CP	3rd-CP	All	1st-CP	2nd-CP	3rd-CP	All	1st-CP	2nd-CP	3rd-CP	All
Model selection												
Model selected ^b	TIM+G	HKY+G	HKY+G	TVM+G	TrNef+G	F81	HKY+G	GTR+I+G	GTR+I+G	K81uf+G	HKY+G	GTR+I+G
freq A	0.4023	0.2142	0.4867	0.3574	–	0.1545	0.4601	0.2861	0.3389	0.1891	0.4764	0.3338
freq C	0.0761	0.1770	0.0377	0.1001	–	0.2509	0.0525	0.1202	0.1137	0.2081	0.0438	0.1042
freq G	0.0977	0.0953	0.0168	0.0619	–	0.1755	0.0144	0.1686	0.1804	0.1278	0.0159	0.1106
freq T	0.4239	0.5135	0.4579	0.4806	–	0.4191	0.4730	0.4251	0.3770	0.4750	0.4640	0.4513
Ti/tv ratio	–	1.2708	6.5309	–	–	–	8.3515	–	–	–	6.2401	–
R [A-C]	1.0000	–	–	2.3944	1.0000	–	–	0.0000	1.7093	1.0000	–	5.9087
R [A-G]	7.8962	–	–	27.3988	1.1580	–	–	23.8169	7.4587	4.3910	–	41.6883
R [A-T]	4.2531	–	–	8.2086	1.0000	–	–	57.1175	7.9487	2.6794	–	39.1278
R [C-G]	4.2531	–	–	5.9980	1.0000	–	–	0.0000	0.0000	2.6794	–	10.3767
R [C-T]	27.9204	–	–	27.3988	82.6756	–	–	277.8802	65.9865	4.3910	–	174.6169
R [G-T]	1.0000	–	–	1.0000	1.0000	–	–	1.0000	1.0000	1.0000	–	1.0000
Proportion of invariable sites (I)	0	0	0	0	0	0	0	0.6694	0.6316	0	0	0.5407
Gamma distr. shape parameter	0.2378	0.2163	0.4522	0.2867	0.1344	–	0.3568	2.6757	0.1665	0.0142	0.4236	1.1771
Composition homogeneity test												
df	36	36	36	36	33	33	33	33	33	33	33	33
I	30.73	18.83	64.55	49.44	34.55	25.33	2.03	34.47	45.98	39.96	17.78	49.67
P (%)	71.73	99.18	0.24	6.72	39.37	82.76	100.00	39.74	6.61	18.84	98.58	3.14
Test of substitution saturation												
Iss	0.3043	0.0650	0.3865	0.1738	0.0668	0.0191	0.4492	0.3878	0.3989	0.1448	0.5325	0.4530
Iss.c (for an asymmetrical tree)	0.7010	0.7047	0.7010	0.7631	0.6975	0.7791	0.6974	0.7447	0.7264	0.7293	0.7263	0.7952
P	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Iss.c (extremely asymm. tree)	0.5193	0.5346	0.5193	0.5974	0.5378	0.7450	0.5376	0.5949	0.5508	0.5649	0.5507	0.6411
P	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0038	0.0000	0.0000	0.0000	0.3736	0.0000

^a CP – codon position; ^b freq – base frequency; Ti/tv ratio – the transition/transversion ratio; R – rate of substitution; TIM – transitional model; HKY – Hasegawa, Kishino, Yano 85 model; TVM – transversional model; TrNef – Tamura-Nei equal frequencies model; F81 – Felsenstein 1981 model; GTR – general timer reversible model; K81uf – two transversion-parameters model 1 unequal frequencies.

Wing (Fig. 1): Dark brown anteriorly, paler posteriorly and curved downward over most of its length. Basal medial-cubital cross vein present; C₁ with 2 subequal setae. Costal vein with 6–8 minute spinules on ventral surface between veins R₂₊₃ and R₄₊₅. Vein R₂₊₃ markedly curved to costa at tip; veins R₄₊₅ and M₁ convergent distally (Fig. 1). Halteres white basally, grey-brown distally.

Legs: Fore femur with 1 row of setae on posterior surface and 1 row of 3–8 setae on ventral surface. Mid tibia with 4–6 strong, suberect setae on basal part of dorsal surface. Apical seta present on mid tibia. Preapical dorsal setae present on all tibiae. Mid and hind tarsomeres with 2 and 1 row(s) of minute cuneiform setulae on ventral surface, respectively; fore and hind first tarsomeres slightly shorter than the rest combined; mid first tarsomere longer than the rest combined.

Abdominal sternites broad, wider than long.

Male terminalia: Epandrium pubescent, mostly with dense setae near posterior margin on each side (Figs 3, 8, 13, 17, 22, 26, 31, 36, 40). Surstylus separated from epandrium. Cercus separated from epandrium, setigerous, but not pubescent (Figs 3, 8, 13, 17, 22, 26, 31, 36, 40). Tenth sternite connected with surstyli basolaterally. Hypandrium anteromedially elongated (Figs 6, 7, 11, 12, 15, 16, 20, 21, 24, 25, 29, 30, 34, 35, 38, 39, 43, 44), with the pair of large membranous flaps fused to each other, sometimes with a few paramedian setae posteroventrally (Figs 15, 16, 24, 25). Parameres (paraphyses) absent (Figs 6, 7, 11, 12, 15, 16, 20, 21, 24, 25, 29, 30, 34, 35, 38, 39, 43, 44). Gonopods (dorsal arch in Bächli et al., 2004) coalesce, forming posteromedian lobe, slightly vaulted,

basolaterally contiguous to posterior ends of hypandrium (Figs 5, 10, 14, 19, 23, 28, 33, 37, 42). Aedeagus broad distally, with tentacle-like setae (marginal fringe in Bächli et al., 2004) on apical margin, basally fused with slender aedeagal apodeme (Figs 6, 7, 11, 12, 15, 16, 20, 21, 24, 25, 29, 30, 34, 35, 38, 39, 43, 44).

Stegana (Steganina) undulata de Meijere, 1911

(Figs 1–7)

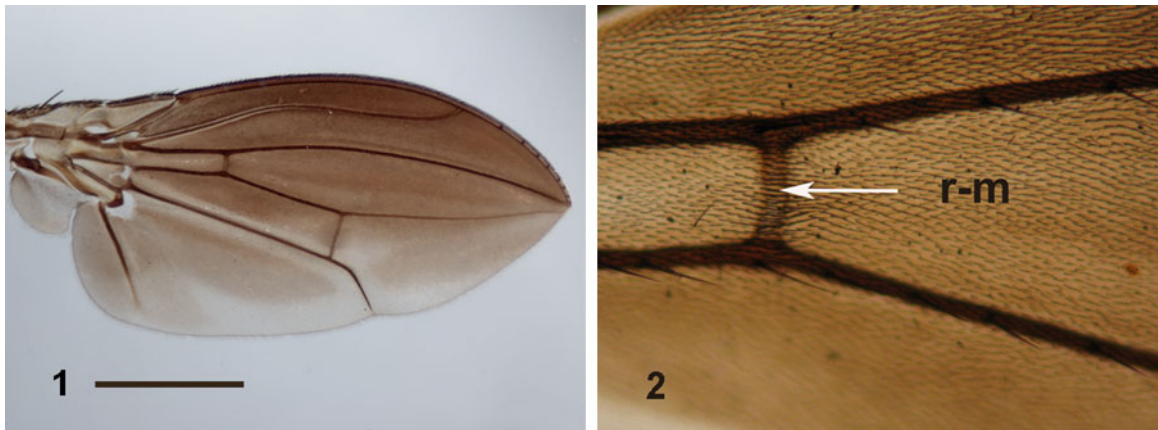
Stegana undulata de Meijere, 1911: 419. Type locality: Indonesia (Java).

Stegana (Steganina) undulata de Meijere: Okada, 1971: 87; Okada & Sidorenko, 1992: 424; Sidorenko, 1998: 296.

Stegana (Stegana) undulata de Meijere: Sidorenko & Okada, 1991: 659.

Diagnosis. Veins R₄₊₅ and M₁ with several setae on basal section of dorsal surface (Figs 1, 2); distal part of 10th sternite nearly rhomboid, about 1.9 times as wide as long (Fig. 5).

Material examined. CHINA: 1♂ (SCAU, No. 120112), Fusui, Chongzuo, Guangxi, 22°31'N, 107°40'E, 230 m, 18.viii.2004, tree trunks, H.W. Chen; 7♂, 8♀ (SCAU, Nos 120113–22), Diaoluoshan, Lingshui, Hainan, 18°10'N, 108°52'E, 1,000 m, 3.xii.2003, tree trunks, H.W. Chen; 3♂, 1♀ (SCAU, Nos 120123–25), Jianfengling, Ledong, Hainan, 18°41'N, 108°52'E, 900 m, 30.xi.2003, 19.v.2004, tree trunks, H.W. Chen; 42♂, 6♀ (SCAU, Nos 120126–70), Mengla, Xishuangbanna, Yunnan, 21°28'N, 101°38'E, 680 m, 10.–12.ix.2002, 21.–24.iv.2007, tree trunks and tussock, H.W. Chen, J.J. Gao, F. Zhao; 14♂, 10♀ (KIZ), Menglun, Xishuangbanna, Yunnan, 21°41'N, 101°25'E, 700 m, 24.–26.xii.2003, 16.–20.iv.2007, tree trunks, H.W. Chen, J.J. Gao, F. Zhao; 2♂, 47♀ (SCAU, Nos 120171–200), Mengyang, Xishuangbanna,



Figs 1, 2. *Stegana (Steganina) undulata* de Meijere, ♂, right wing dorsal. 1 – overview, scale bar = 1 mm; 2 – basal section of R_{4+5} and M_1 , each bearing several setae.

Yunnan, 22°20'N, 100°51'E, 700 m, 14.–15.xi.2002, tree trunks, H.W. Chen. MYANMAR: 1♂ (SEHU), Rangoon (Yangon), 18.xii.1981, M.J. Toda. INDONESIA: 5♂ (3♂ in MZB, 2♂ in SEHU), Bogor, Java, 8.xii.1996, underside of fallen logs, M.J. Toda.

Distribution. China (Guangxi, Hainan, Yunnan), Myanmar (Yangon), Indonesia (Java, Sumatra, Kalimantan).

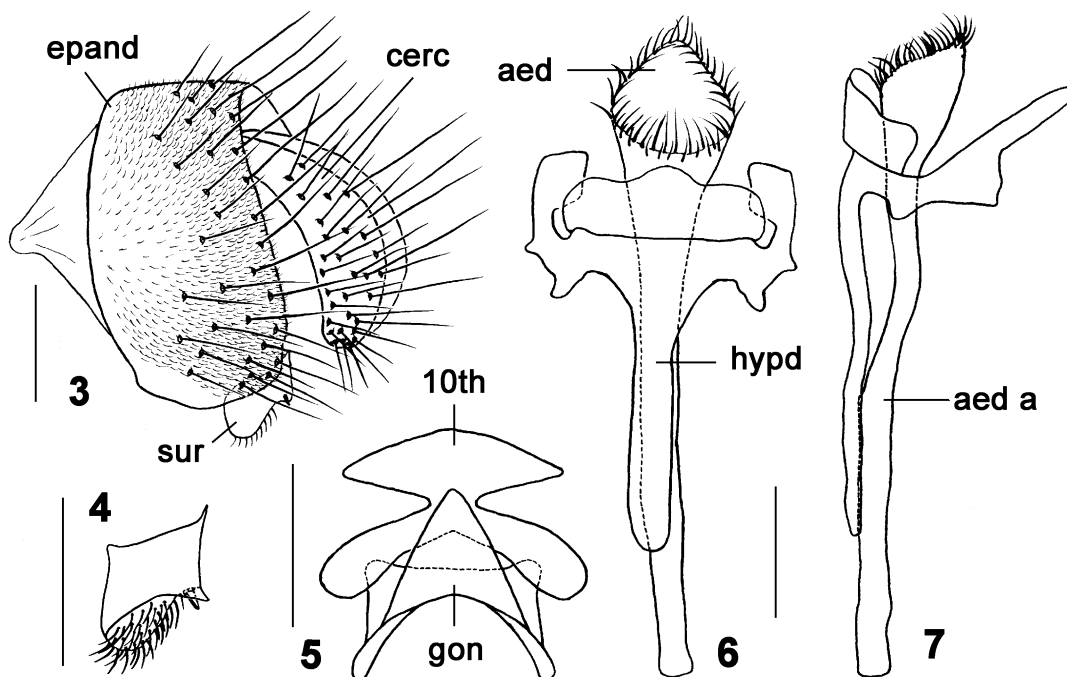
***Stegana (Steganina) melanocheilota* Chen & Chen, sp. n.**

(Figs 8–12)

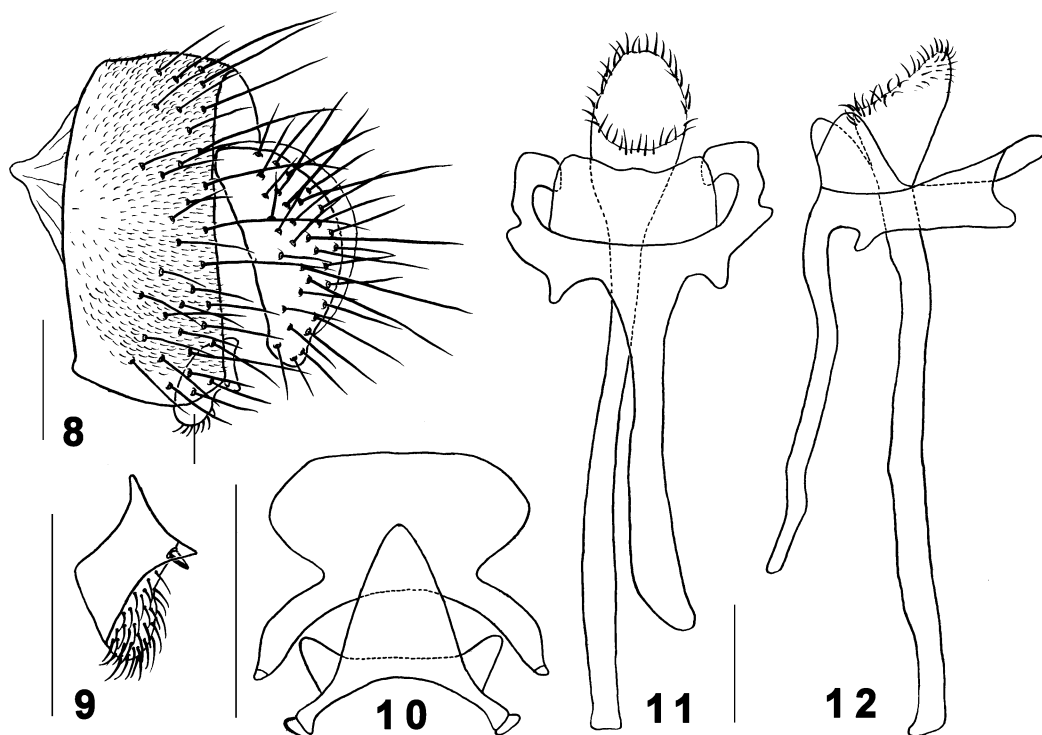
Diagnosis. Different from *S. undulata* in that the distal part of 10th sternite is strongly broadened, transversely oval, about 1.9 times as wide as long (Fig. 10) and the

distal part of aedeagus slightly rounded in ventral view (Fig. 11).

Description. Male and Female: Frons orange yellow, medially brown. Fronto-orbital plate orange yellow. Pedicel yellow; first flagellomere almost black. Face black on upper 1/2, yellow on lower 1/2. Clypeus black. Palpus yellow basally, black distally. Mesonotum yellowish brown, with 2 pairs of yellow longitudinal stripes submedially and a few grey-yellow patches laterally (anterior to wing base). Postpronotal lobe brown on upper 1/5, white on lower 4/5. Katepisternum white. Scutellum brown. Costal vein with 8–10 minute spinules on ventral surface between veins R_{2+3} and R_{4+5} . Legs brown, white on basal parts of all femora and distal part of mid tibia,



Figs 3–7. *Stegana (Steganina) undulata* de Meijere, ♂. 3 – epandrium (epand), surstylus (sur) and cercus (cerc) (lateral view); 4 – surstylus; 5 – 10th sternite (10st) and gonopods (gon) (ventral view); 6 – hypandrium (hypd), aedeagus (aed) and aedeagal apodeme (aed a) (ventral view); 7 – ditto (lateral view). Scale bars = 0.1 mm.



Figs 8–12. *Stegana (Steganina) melanocheilota* Chen & Chen, sp. n., ♂. 8 – epandrium, surstylus and cercus; 9 – surstylus; 10 – 10th sternite and gonopods; 11 – hypandrium, aedeagus and aedeagal apodeme; 12 – ditto. For orientation, see Figs 3–7. Scale bars = 0.1 mm.

black on fore and mid knees. Fore femur with 6 setae on distal part of ventral surface. Abdominal 1st to 5th tergites black medially, yellow laterally; 6th tergite nearly black. Sternites brown.

Male terminalia: Hypandrium anteromedially remarkably elongated, 2.4 times longer than width of epandrium and lacking paramedian setae (Figs 11, 12). Gonopods slightly triangular (Fig. 10). Aedeagus about 0.25 times as long as aedeagal apodeme (Fig. 12).

Measurements. BL = 3.45 mm in holotype (range in 2♂ and 3♀ paratypes: 3.35–3.85 mm in ♂, 3.20–3.70 mm in ♀), ThL = 1.68 mm (1.80–1.90 mm in ♂, 1.68–1.19 mm in ♀), WL = 3.05 mm (3.30–3.40 mm in ♂, 3.25–3.30 mm in ♀), WW = 1.30 mm (1.15–1.30 mm in ♂, 1.05–1.37 mm in ♀), arb = 11/8 (10–11/7–8), avd = 0.77 (0.71–0.85), adf = 1.63 (1.50–2.14), flw = 1.75 (1.75–2.14), FW/HW = 0.41 (0.40–0.44), ch/o = 0.15 (0.15–0.18), prorb = 0.88 (0.89–0.94), rcorb = 0.75 (0.77–0.89), vb = 0.63 (0.59–0.73), dcl = 0.47 (0.48), sctl = 1.37, sterno = 0.95 (0.81–0.94), orbito = 2.20 (1.83–2.20), dep = 0.21 (0.19–0.24), sctlp = 2.20 (1.91–2.30), C = 1.92 (1.88–2.20), 4c = 1.15 (0.97–2.23), 4v = 1.79 (1.63–2.00), 5x = 1.50 (1.33–1.62), ac = 9.50 (8.75–10.25), M = 0.55 (0.44–0.68), C3F = 0.70 (0.65–0.74).

Type material. Holotype ♂ (SCAU, No. 120201), CHINA: Menglun, Xishuangbanna, Yunnan, 17.iv.2007, ex tussock, J.J. Gao. Paratypes: CHINA: 2♂, 3♀ (1♂, 1♀ in KIZ, 1♂, 2♀ in SCAU, Nos 120202–04), same data as holotype, 17.–18.iv.2007, tree trunks and tussock, H.W. Chen, J.J. Gao, F. Zhao.

Etymology. A combination of the Greek words melas + cheilos referring to the black clypeus.

Distribution. China (Yunnan).

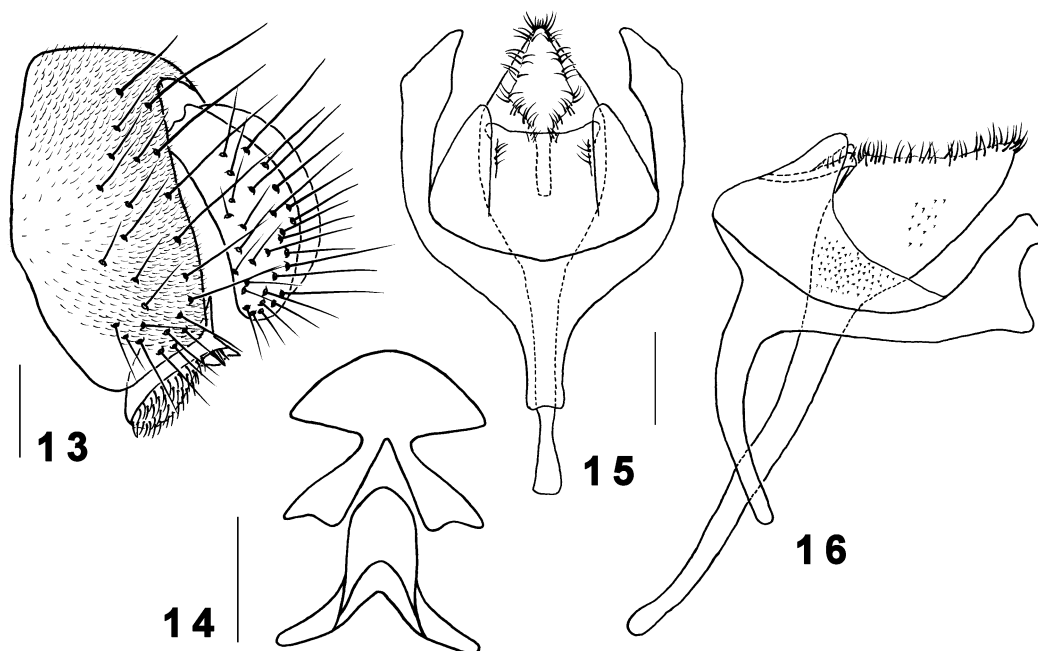
Stegana (Steganina) flavipalpata Chen & Chen, sp. n.

(Figs 13–16)

Diagnosis. Differs from other species of the *undulata* group in the yellow scutellum with brown stripes or patches in the male, dark brown with yellow patch at tip in female, and numerous serrated, minute processes at the base of the aedeagus (Fig. 16).

Description. Male and female. Frons black, with orange yellow band submedially. Fronto-orbital plate orange yellow. Pedicel black basally, orange yellow distally; first flagellomere almost black. Face black on upper 1/2, yellow on lower 1/2. Clypeus yellow. Palpus yellow. Mesonotum yellowish brown, with a broad black stripe medially and a few brown patches laterally (anterior to wing base). Postpronotal lobe white on anterior 1/2, brown on posterior 1/2. Katepisternum white. Costal vein with 8–11 minute spinules on ventral surface between veins R_{2+3} and R_{4+5} . Veins R_{4+5} and M_1 convergent distally, as in *S. undulata* (Fig. 1). Legs white with black knee articulations. Fore femur with 8 setae on ventral surface. Mid tibia with 5 strong setae on basal part of dorsal surface. Abdominal tergites black except for 2nd and 3rd tergites yellow laterally. Sternites dark brown.

Male terminalia: Hypandrium anteromedially elongated, about 1.28 times as long as width of epandrium and with a few paramedian setae posteroventrally (Figs 15, 16). Distal part of 10th sternite umbrella-like, about 2.4 times as wide as long (Fig. 14). Gonopods slightly rounded posteromedially (Fig. 14). Aedeagus about 0.63 times as long as aedeagal apodeme (Fig. 16).



Figs 13–16. *Stegana (Steganina) flavipalpata* Chen & Chen, sp. n., ♂. 13 – epandrium, surstylus and cercus; 14 – 10th sternite and gonopods; 15 – hypandrium, aedeagus and aedeagal apodeme; 16 – ditto. For orientation, see Figs 3–7. Scale bars = 0.1 mm.

Measurements. BL = 3.67 mm in holotype (range in 4♂ and 3♀ paratypes: 3.40–3.75 mm in ♂, 3.00–4.00 mm in ♀), ThL = 2.22 mm (2.20–2.35 mm in ♂, 2.03–2.24 mm in ♀), WL = 4.20 mm (4.20–4.55 mm in ♂, 3.75–4.30 mm in ♀), WW = 1.55 mm (1.63–1.90 mm in ♂, 1.53–1.70 mm in ♀), arb = 9/7 (9/6–7), avd = 0.79 (0.71–0.85), adf = 1.75 (1.44–2.00), flw = 2.00 (1.50–2.12), FW/HW = 0.42 (0.42–0.51), ch/o = 0.18 (0.15–0.20), pror = 1.12 (0.85–1.12), rcorb = 0.82 (0.73–0.86), vb = 0.62 (0.54–0.74), dcl = 0.58 (0.41–0.56), sctl = 1.22 (1.25–1.57), sterno = 0.77 (0.64–0.86), orbito = 1.83 (1.83–2.20), dcp = 0.26 (0.26–0.29), sctlp = 1.67 (1.50–2.00), C = 1.61 (1.58–1.76), 4c = 1.50 (1.16–1.50), 4v = 1.82 (1.70–1.95), 5x = 1.46 (1.22–1.47), ac = 10.20 (9.80–10.60), M = 0.56 (0.42–0.61), C3F = 0.74 (0.71–0.78).

Type material. Holotype ♂ (SCAU, No. 120205), CHINA: Wuliangshan, Nanjian, Yunnan, 24°31'N, 101°40'E, 2,230 m, 25.vii.2006, tree trunk, T. Li. Paratypes: CHINA: 1♂ (SCAU, No. 120206), same data as holotype; 2♂, 3♀ (1♂, 1♀ in KIZ, 1♂, 2♀ in SCAU, Nos 120207–09), Wuliangshan, Jingdong, Yunnan, 4.–5.viii.2006, tree trunks, H.L. Cao, H.Z. Cao, T. Li; 1♂ (SCAU, No. 120210), Jiaoye Park (Qiongzhusi), Kunming, Yunnan, 19.viii.2006, tree trunk, H.L. Cao.

Etymology. A combination of the Latin words flavus + palpus, referring to the yellow palpus.

Distribution. China (Yunnan).

***Stegana (Steganina) leucothorax* Chen & Chen, sp. n.**
(Figs 17–21)

Diagnosis. Differs from *S. melanocheilota* as it has a yellow clypeus and the distal part of 10th sternite slightly transversely oval, 1.7 times as wide as long (Fig. 19).

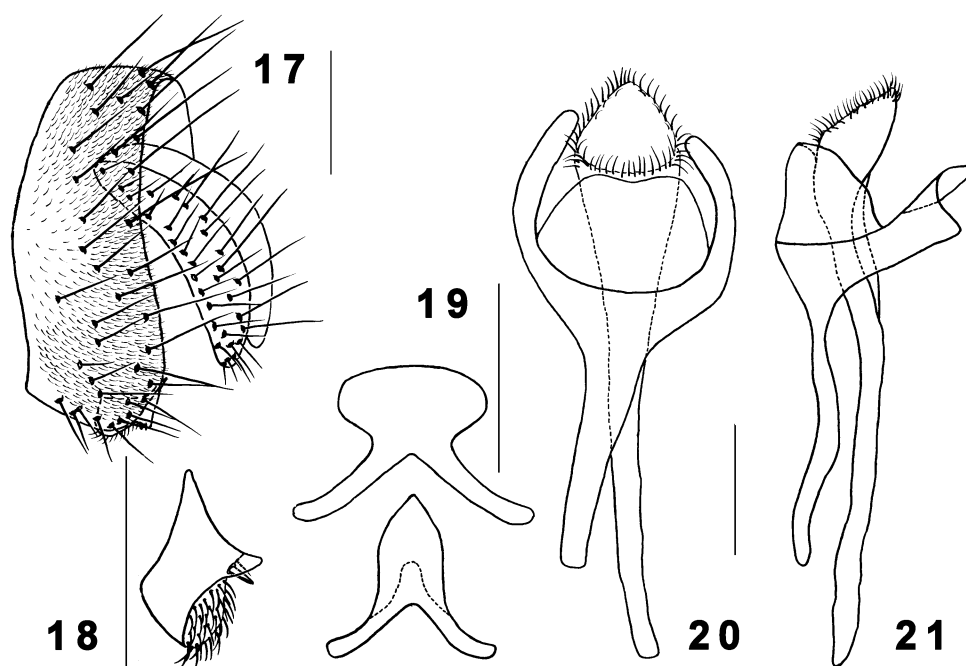
Description. Male and female. Frons orange yellow, with black stripes sublaterally. Fronto-orbital plate orange yellow. Pedicel yellow; first flagellomere almost black, greyish yellow basally. Face black on upper 1/2, yellow on lower 1/2. Palpus yellow basally, black distally. Mesonotum brown, with 1 yellow stripe medially and 3

pairs of dark brown stripes submedially and a few greyish yellow patches laterally (anterior to wing base). Postpronotal lobe brown on anterior 2/5, white on posterior 3/5. Katepisternum white. Scutellum brown. Costal vein with 8–10 minute spinules on ventral surface between veins R_{2+3} and R_{4+5} . Legs brown, white on basal parts of all femora and distal part of mid tibia, black on fore and mid knees. Abdominal tergites 1 to 5 black medially, yellow laterally; 6th tergite nearly black. Sternites dark brown.

Male terminalia: Hypandrium anteromedially elongated, about 2.47 times as long as width of epandrium, without paramedian setae posteroventrally (Figs 20, 21). Gonopods shovel-like and acute apically (Fig. 19). Distal part of aedeagus triangular in ventral view (Fig. 20), without serrated, minute processes, about 0.3 times as long as aedeagal apodeme (Fig. 21).

Measurements. BL = 3.00 mm in holotype (range in 4♂ and 5♀ paratypes: 2.75–3.15 mm in ♂, 2.90–3.25 mm in ♀), ThL = 1.70 mm (1.56–1.75 mm in ♂, 1.64–1.86 mm in ♀), WL = 2.85 mm (2.90–3.05 mm in ♂, 2.30–3.20 mm in ♀), WW = 1.36 mm (0.96–1.28 mm in ♂, 1.10–1.32 mm in ♀), arb = 13/7 (11–13/7–8), avd = 0.77 (0.77–0.85), adf = 2.17 (1.63–2.00), flw = 2.50 (1.85–2.50), FW/HW = 0.39 (0.43–0.47), ch/o = 0.15 (0.15–0.16), pror = 1.00 (0.88–1.00), rcorb = 0.94 (0.81–0.88), vb = 0.63 (0.56–0.75), dcl = 0.50 (0.39–0.59), sctl = 1.60 (1.40–1.70), sterno = 0.90 (0.81–0.91), orbito = 2.20 (1.83–2.50), dcp = 0.26 (0.23–0.30), sctlp = 2.00 (1.73–2.11), C = 1.87 (1.76–2.16), 4c = 1.18 (1.03–1.19), 4v = 1.70 (1.65–1.79), 5x = 1.31 (1.07–1.45), ac = 13.00 (11.00–13.67), M = 0.52 (0.47–0.56), C3F = 0.78 (0.76–0.78).

Type material. Holotype ♂ (SCAU, No. 120211), CHINA: Wangtianshu, Mengla, Xishuangbanna, Yunnan, 10.ix.2002, tree trunk, H.W. Chen. Paratypes: CHINA: 15♂, 15♀ (5♂, 5♀ in KIZ, 8♂, 8♀ in SCAU, Nos 120212–27, 2♂, 2♀ in SEHU), same data as holotype, 10.–11.ix.2002, 21.–25.iv.2007, tree trunks and tussock, H.W. Chen, J.J. Gao, F. Zhao; 3♂ (SCAU,



Figs 17–21. *Stegana (Steganina) leucothorax* Chen & Chen, sp. n., ♂. 17 – epandrium, surstylus and cercus; 18 – surstylus; 19 – 10th sternite and gonopods; 20 – hypandrium, aedeagus and aedeagal apodeme; 21 – ditto. For orientation, see Figs 3–7. Scale bars = 0.1 mm.

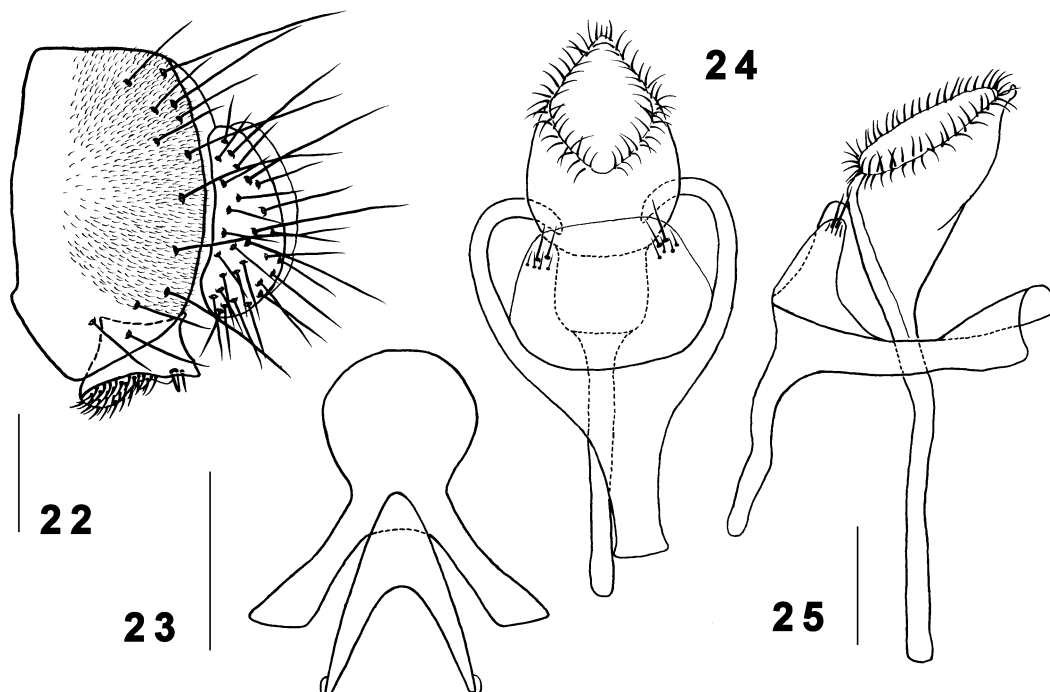
Nos 120228–30), Menglun, Xishuangbanna, Yunnan, 13.–14.ix.2002, tree trunks, H.W. Chen; 14♂, 12♀ (SCAU, Nos 120231–56), Mengyang, Xishuangbanna, Yunnan, 14.–15.ix.2002, tree trunks, H.W. Chen.

Etymology. A combination of the Greek words leucon + thorax, referring to the white pleura.

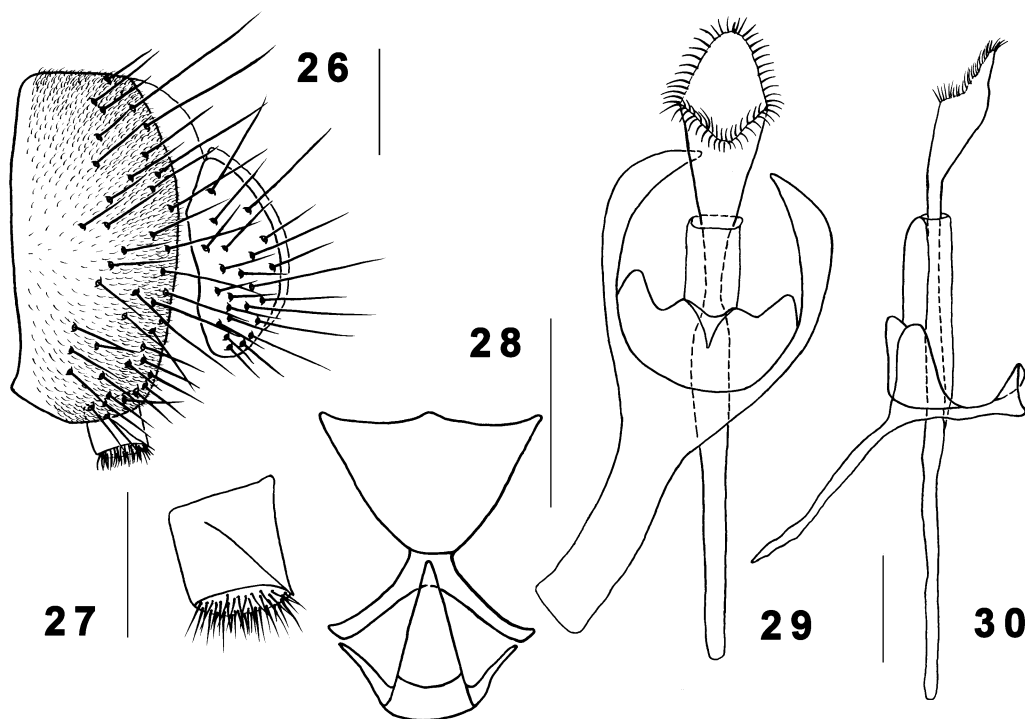
Distribution. China (Yunnan).

***Stegana (Steganina) flaviclypeata* Chen & Chen, sp. n.**
(Figs 22–25)

Diagnosis. Separated from *S. flavipalpata* by having a yellow clypeus, the scutellum dark brown, yellow at tip, the distal part of 10th sternite nearly rounded, 0.85 times as wide as long (Fig. 23), and the aedeagus lacking serrated minute processes (Fig. 25).



Figs 22–25. *Stegana (Steganina) flaviclypeata* Chen & Chen, sp. n., ♂. 22 – epandrium, surstylus and cercus; 23 – 10th sternite and gonopods; 24 – hypandrium, aedeagus and aedeagal apodeme; 25 – ditto. For orientation, see Figs 3–7. Scale bars = 0.1 mm.



Figs 26–30. *Stegana (Steganina) flaviscutellata* Chen & Chen, sp. n., ♂. 26 – epandrium, surstylus and cercus; 27 – surstylus; 28 – 10th sternite and gonopods; 29 – hypandrium, aedeagus and aedeagal apodeme; 30 – ditto. For orientation, see Figs 3–7. Scale bars = 0.1 mm.

Description. Male. Frons orange yellow, with black stripes sublaterally. Fronto-orbital plate orange yellow. Pedicel and first flagellomere yellow, with black pubescence along margin. Face black, with yellow band medially. Palpus yellow. Mesonotum brown to dark brown, with yellow stripes and patches laterally (anterior to wing bases). Postpronotal lobe whitish yellow on anterior 2/5, brown on posterior 3/5. Katepisternum whitish yellow. Costal vein with 9–11 minute spinules on ventral surface between veins R_{2+3} and R_{4+5} . Legs mostly white, all knee articulations black. Abdominal tergites 1 to 5 brown medially, pale laterally; 6th tergite nearly black. Sternites yellow, slightly brownish laterally.

Male terminalia: Hypandrium anteromedially slightly elongated, about 1.2 times as long as width of epandrium, with a few paramedian setae posteroventrally (Figs 24, 25). Gonopods nearly triangular and slightly rounded apically (Fig. 23). Aedeagus very expanded apically in ventral view, about 0.63 times as long as aedeagal apodeme (Figs 24, 25).

Measurements. BL = 3.47 mm in holotype, ThL = 1.85 mm, WL = 3.88 mm, WW = 1.40 mm, arb = 7/6, avd = 0.90, adf = 1.25, flw = 1.75, FW/HW = 0.47, ch/o = 0.21, pror = 1.17, rcorb = 0.83, vb = 0.50, dcl = 0.52, sctl = 1.32, sterno = 0.86, orbito = 1.67, dcp = 0.31, sculp = 1.90, C = 2.70, 4c = 1.05, 4v = 1.61, 5x = 1.47, ac = 9.20, M = 0.50, C3F = 0.73.

Type material. Holotype ♂ (SCAU, No. 120257), CHINA: Moxi, Luding, Sichuan, 29°39'N, 102°06'E, 1,100 m, 17.ix.2005, tree trunks, H.W. Chen. Paratypes: 1 ♂, 1 ♀ (SCAU, Nos 120258, 59), Wuliangshan, Jingdong, Simao, Yunnan, 4.–5.viii.2006, tree trunks, H.L. Cao, H.Z. Cao.

Etymology. A combination of the Latin words flavus + clypeus, referring to the yellow clypeus.

Distribution. China (Sichuan, Yunnan).

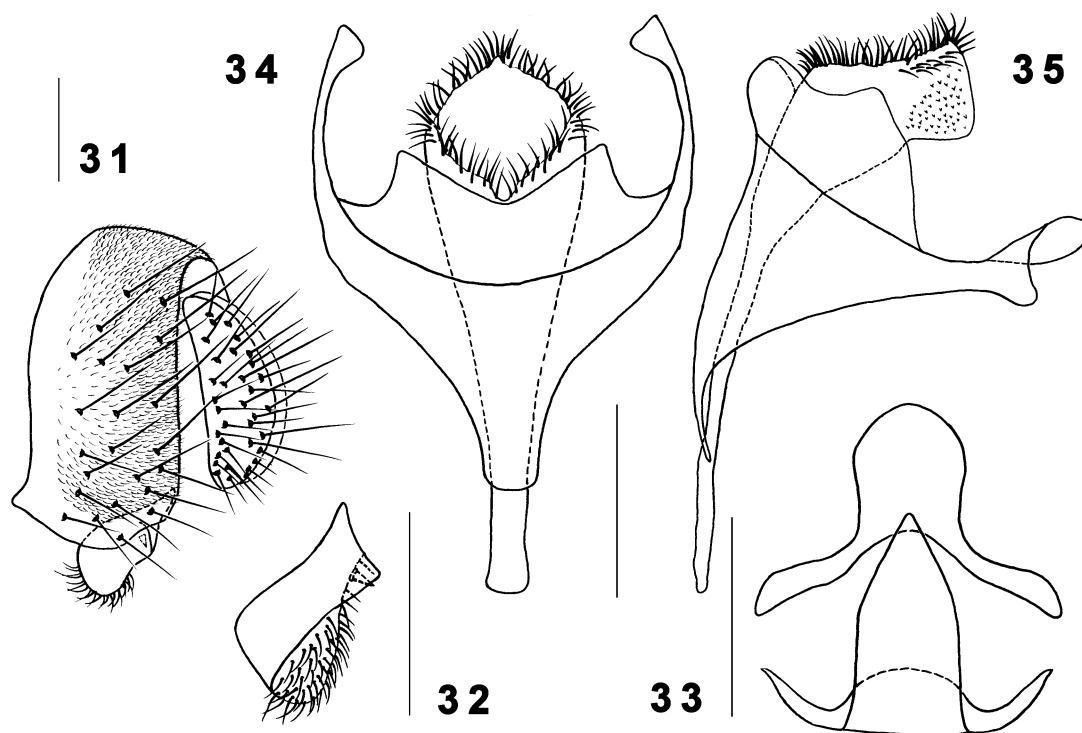
Stegana (Steganina) flaviscutellata Chen & Chen, sp. n. (Figs 26–30)

Diagnosis. Differs from other species of the *undulata* group in having a surstylus without preniseta (Fig. 27) and in the distal part of 10th sternite infundibular in ventral view (Fig. 28).

Description. Male and female. Frons and fronto-orbital plate orange yellow. Pedicel orange yellow; basal 1/2 of first flagellomere yellow, distal 1/2 black. Face yellow, black on lower margin. Clypeus black. Palpus yellow basally, black distally. Mesonotum yellow, with dark brown stripes and patches laterally. Postpronotal lobe yellow on anterior 3/5, brown on posterior 2/5. Katepisternum brown, slightly yellowish ventrally. Scutellum yellow. Costal vein with 9–11 minute spinules on ventral surface between veins R_{2+3} and R_{4+5} . Legs black except for all tarsomeres brownish. Fore femur with 6–7 setae on ventral surface. Mid tibia with 4 strong setae on basal part of dorsal surface. Abdominal tergites and sternites nearly entirely brown.

Male terminalia: Hypandrium anteromedially elongated, about 1.56 times as long as width of epandrium, without paramedian setae posteroventrally (Figs 29, 30). Gonopods narrow distally, subacute apically (Fig. 28). Aedeagus lacks serrated, minute processes, about 0.29 times as long as aedeagal apodeme (Figs 29, 30).

Measurements. BL = 3.15 mm in holotype (range in 4 ♂ and 5 ♀ paratypes: 2.90–3.65 mm in ♂, 3.60–4.15 mm in ♀), ThL = 1.64 mm (1.64–1.92 mm in ♂, 1.86–2.20 mm in ♀), WL = 2.80 mm (2.75–3.35 mm in ♂, 3.40–4.1 mm in ♀), WW = 1.20 mm



Figs 31–35. *Stegana (Steganina) nigriclypeata* Chen & Chen, sp. n., ♂. 31 – epandrium, surstylus and cercus; 32 – surstylus; 33 – 10th sternite and gonopods; 34 – hypandrium, aedeagus and aedeagal apodeme; 35 – ditto. For orientation, see Figs 3–7. Scale bars = 0.1 mm.

(1.20–1.36 mm in ♂, 1.38–1.58 mm in ♀), arb = 12/6 (12/7), avd = 0.83 (0.75–0.83), adf = 2.14 (1.87–2.28), flw = 2.14 (1.87–2.28), FW/HW = 0.48 (0.46–0.53), ch/o = 0.16 (0.15–0.17), prorb = 0.88 (0.88–1.12), rcorb = 0.75 (0.67–0.89), vb = 0.69 (0.70–0.76), dcl = 0.50 (0.33–0.50), sctl = 1.44 (1.45–1.72), sterno = 0.80 (0.78–0.86), orbito = 2.50 (2.20–2.50), dcp = 0.24 (0.17–0.24), sctlp = 1.54 (1.81–2.40), C = 1.81 (1.92–2.21), 4c = 1.19 (1.16–1.33), 4v = 1.68 (1.71–2.11), 5x = 2.00 (1.33–1.91), ac = 18.5 (13.00–23.00), M = 0.65 (0.54–0.64), C3F = 0.82 (0.78–0.86).

Type material. Holotype ♂ (KPSP), MALAYSIA: Poring, Sabah, 16.iii.1999, tree trunk, M.J. Toda. Paratypes: MALAYSIA: 13♂, 7♀ (5♂, 2♀ in ITBC; 4♂, 2♀ in KPSP; 2♂, 2♀ in SEHU; 2♂, 1♀ in SCAU, Nos 120260–62), same data as holotype; 2♀ (KPSP), Mt. Kinabalu, Sabah, Malaysia, 10.–11.iii.1999, fallen logs, M.J. Toda.

Etymology. A combination of the Latin words flavum + scutellum, referring to the yellow scutellum.

Distribution. Malaysia (Sabah).

***Stegana (Steganina) nigriclypeata* Chen & Chen, sp. n.**
(Figs 31–35)

Diagnosis. Differs from *S. flavipalpata* in having an aedeagus that protrudes posterodorsally, with serrated, minute processes covering the protrusion (Fig. 35).

Description. Male: Frons brown. Fronto-orbital plate orange yellow. Pedicel orange yellow; first flagellomere yellow on basal 2/3, black on distal 1/3. Face yellow, black on lower margin. Clypeus black. Palpus almost black. Mesonotum yellowish brown, without stripes and patches. Postpronotal lobe yellowish brown. Katepisternum dark brown. Scutellum yellow. Costal vein with 9–10 minute spinules on ventral surface between veins

R₂₊₃ and R₄₊₅. Legs greyish yellow, white on basal part of fore femur and distal part of mid tibia, black on distal part of fore femur and whole of mid and hind femora. Fore femur with 3 setae on distal part of ventral surface. Abdominal tergites nearly entirely brown, sternites yellow.

Male terminalia: Distal part of 10th sternite slightly rounded, 0.56 times as wide as long (Fig. 33). Hypandrium anteromedially slightly elongated, about 1.39 times as long as width of epandrium, without paramedian setae posteroventrally (Figs 34, 35). Gonopods almost triangular distally (Fig. 33). Aedeagus about 0.72 times as long as aedeagal apodeme (Figs 34, 35).

Measurements. BL = 2.43 mm in holotype, ThL = 1.12 mm, WL = 2.13 mm, WW = 1.20 mm, arb = 14/5, avd = 0.82, adf = 0.84, flw = 1.88, FW/HW = 0.57, ch/o = 0.20, prorb = 1.29, rcorb = 0.71, vb = 0.58, dcl = 0.37, sctl = 2.13, sterno = 1.33, orbito = 2.14, dcp = 0.21, sctlp = 2.40, C = 2.18, 4c = 1.00, 4v = 1.82, 5x = 1.81, ac = 22.00, M = 0.66, C3F = 0.87.

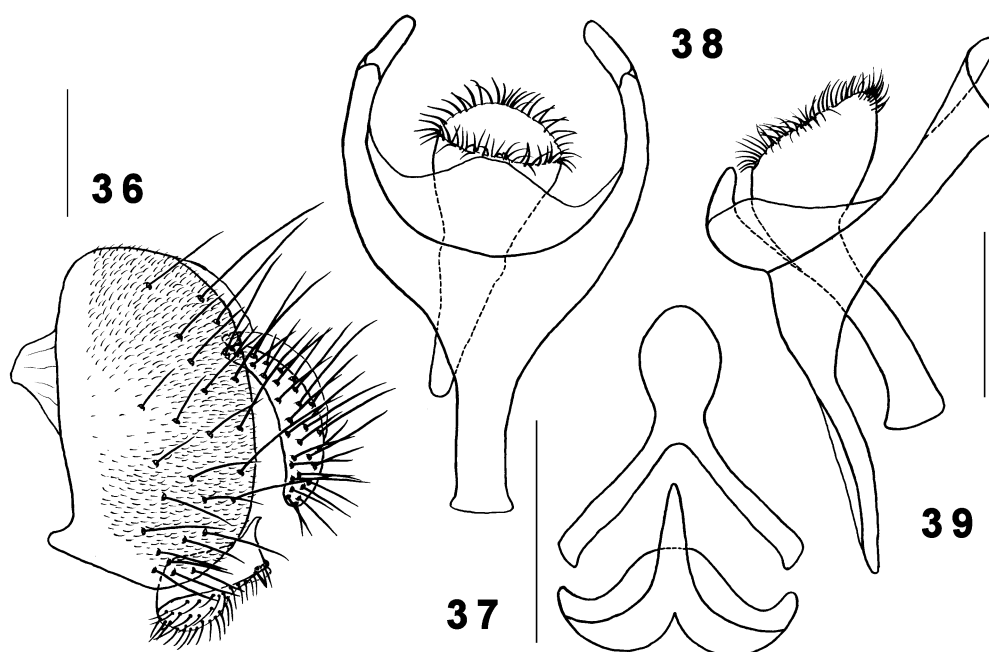
Type material. Holotype ♂ (KPSP), MALAYSIA: Poring, Sabah, 29.xii.1998, fallen log, M.J. Toda.

Etymology. A combination of the Latin words niger + clypeus, referring to the black clypeus.

Distribution. Malaysia (Sabah).

***Stegana (Steganina) nigripalpata* Chen & Chen, sp. n.**
(Figs 36–39)

Diagnosis. Differs from *S. nigriclypeata* in having the distal part of 10th sternite slightly oblong, 0.33 times as wide as long (Fig. 37), and the gonopods narrow distally, acute apically (Fig. 37).



Figs 36–39. *Stegana (Steganina) nigripalpata* Chen & Chen, sp. n., ♂. 36 – epandrium, surstylus and cercus; 37 – 10th sternite and gonopods; 38 – hypandrium, aedeagus and aedeagal apodeme; 39 – ditto. For orientation, see Figs 3–7. Scale bars = 0.1 mm.

Description. Male. Frons brown. Fronto-orbital plate orange yellow. Pedicel orange yellow; first flagellomere yellow on basal 2/3, black on distal 1/3. Face yellow, brown on lower corners. Clypeus black. Palpus predominantly black. Mesonotum yellow, slightly brownish laterally, without stripes and patches. Postpronotal lobe yellowish brown. Katepisternum brown, slightly yellow ventrally. Scutellum yellow. Costal vein with 9 minute spinules on ventral surface between veins R_{2+3} and R_{4+5} . Legs brown except for greyish yellow distal parts of mid and hind tibiae and all tarsomeres. Fore femur with 3 setae on distal part of ventral surface. Mid tibia with 6 strong setae on basal part of dorsal surface. Abdominal tergites and sternites nearly entirely brown.

Male terminalia: Hypandrium anteromedially elongated, about 1.67 times as long as width of epandrium, without paramedian setae (Figs 38, 39). Aedeagus without serrated, minute processes, about 0.7 times as long as aedeagal apodeme (Figs 38, 39).

Measurements. BL = 2.74 mm in holotype, ThL = 1.48 mm, WL = 2.56 mm, WW = 0.98 mm, arb = 15/5, avd = 0.92, adf = 1.50, flw = 1.88, FW/HW = 0.47, ch/o = 0.16, prorb = 1.33, rcorb = 0.67, vb = 0.50, dcl = 0.60, sctl = 1.70, sterno = 1.33, orbito = 2.00, dcp = 0.15, sctlp = 2.00, C = 1.97, 4c = 1.10, 4v = 1.97, 5x = 1.90, ac = 32.00, M = 0.66, C3F = 0.74.

Type material. Holotype ♂ (KPSP), MALAYSIA: Poring, Sabah, 16.iii.1999, tree trunk, M.J. Toda.

Etymology. A combination of the Latin words niger + palpus, referring to the black palpus.

Distribution. Malaysia (Sabah).

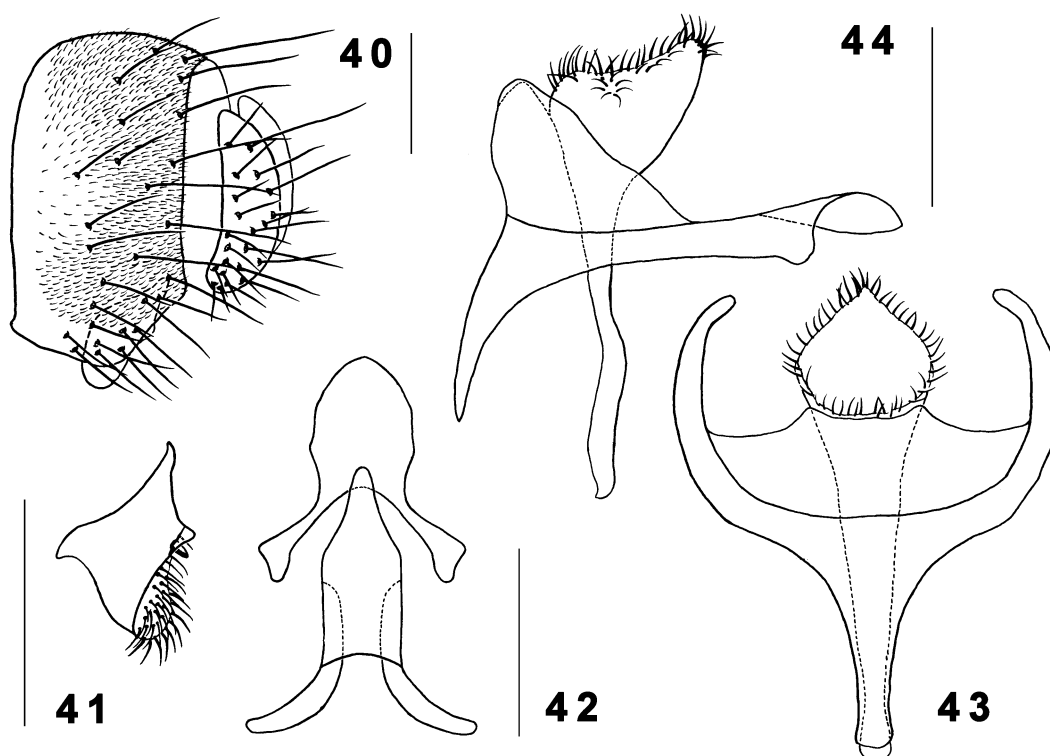
***Stegana (Steganina) melanothorax* Chen & Chen, sp. n.** (Figs 40–44)

Diagnosis. Differs from *S. leucothorax* in having an entirely black clypeus and katepisternum and predominantly black palpus.

Description. Male and female. Frons black, with an orange yellow band submedially. Fronto-orbital plate orange yellow. Pedicel orange yellow; first flagellomere almost black. Face black, yellow on lower margin. Mesonotum dark brown, laterally with yellow stripes and patches. Postpronotal lobe brown. Scutellum brown. Costal vein with 7–8 minute spinules on ventral surface between veins R_{2+3} and R_{4+5} . Legs dark brown, whitish yellow on distal parts of mid and hind tibiae, greyish yellow on all 2nd to 5th tarsomeres. Fore femur with 4–5 setae on distal part of ventral surface. Mid tibia with 4–5 strong setae on basal part of dorsal surface. Abdominal tergites and sternites nearly entirely dark brown.

Male terminalia. Distal part of 10th sternite slightly oblong, 0.8 times as wide as long (Fig. 42). Hypandrium anteromedially elongated, about 1.3 times as long as width of epandrium, without paramedian setae (Figs 43, 44). Gonopods roughly triangular distally, with narrowly rounded apex (Fig. 42). Aedeagus without serrated, minute processes, about 0.64 times as long as aedeagal apodeme (Figs 43, 44).

Measurements. BL = 3.27 mm in holotype (range in 3 ♂ and 3 ♀ paratypes: 2.88–3.36 mm in ♂, 2.84–3.28 mm in ♀), ThL = 1.68 mm (1.59–1.72 mm in ♂, 1.42–1.78 mm in ♀), WL = 3.40 mm (2.76–3.36 mm in ♂, 2.53–2.93 mm in ♀), WW = 1.52 mm (1.32–1.50 mm in ♂, 1.24–1.47 mm in ♀), arb = 12/8 (12–13/7–8), avd = 0.92 (0.77–0.92), adf = 1.85 (1.67–2.00), flw = 1.85 (1.71–2.33), FW/HW = 0.43 (0.40–0.46), ch/o = 0.17 (0.15–0.17), prorb = 0.78 (0.71–0.94), rcorb = 0.61 (0.57–0.94), vb = 0.69 (0.65–0.76), dcl = 0.80 (0.43–0.81), sctl = 1.80 (1.06–1.81), sterno = 0.74 (0.74–0.94), orbito = 1.70 (1.67–2.20), dcp = 0.17 (0.15–0.24), sctlp = 2.33 (1.45–2.29), C = 2.02 (1.79–2.17), 4c = 1.24 (1.00–1.26), 4v = 1.94 (1.25–1.85), 5x = 1.27 (1.21–1.50), ac = 20.50 (18.50–20.50), M = 0.58 (0.47–0.61), C3F = 0.64 (0.58–0.73).



Figs 40–44. *Stegana (Steganina) melanothorax* Chen & Chen, sp. n., ♂. 40 – epandrium, surstylus and cercus; 41 – surstylus; 42 – 10th sternite and gonopods; 43 – hypandrium, aedeagus and aedeagal apodeme; 44 – ditto. For orientation, see Figs 3–7. Scale bars = 0.1 mm.

Type material. Holotype ♂ (SCAU, No. 120263), CHINA: Wangtianshu, Mengla, Xishuangbanna, Yunnan, 10.ix.2002, tree trunk, H.W. Chen. Paratypes: CHINA: 2♀, same data as holotype (SCAU, Nos 120264, 65); 3♂, 1♀ (1♂, 1♀ in KIZ, 2♂ in SCAU, Nos 120266, 67), Menglun, Xishuangbanna, Yunnan, 13.–14.ix.2002, tree trunks, H.W. Chen.

Etymology. A combination of the Greek words melas + thorax, referring to the black katapisternum.

Distribution. China (Yunnan).

Key to the species of the *undulata* group

- 1 Surstylus mostly with 1 small acute prensiseta submedially on inner margin (absent in *S. melanothorax*), only distally with dense setae; distal part of 10th sternite expanded to lobate (the *undulata* group). 2
- Surstylus usually without or with only 1 prensiseta apically, or (in the *shirozui* group) with 1 row of 5–8 prensisetae submedially on inner margin, with several setae basally and sparse setae distally; distal part of 10th sternite not expanded. other *Steganina* species
- 2 Veins R_{4+5} and M_1 with several setae on basal section of dorsal surface. *S. undulata* de Meijere
- Veins R_{4+5} and M_1 without setae on basal section. 3
- 3 Katapisternum white to white-yellow. 4
- Katapisternum brown to black, sometimes pale ventrally. 7
- 4 Face black, with yellow band medially; distal part of 10th sternite nearly rounded, its length distinctly greater than width. *S. flavicypeata* Chen & Chen, sp. n.
- Face black on upper 1/2, yellow on lower 1/2; distal part of 10th sternite broadened, distinctly shorter than wide. 5
- 5 Palpus entirely yellow; scutellum yellow with brown stripes or patches in male, dark brown with yellow tip in female; hypandrium with paramedian setae posteroventrally;

- aedeagus with numerous, serrated, minute processes.
- *S. flavipalpata* Chen & Chen, sp. n.
- Palpus yellow basally, black distally; scutellum brown; hypandrium without paramedian setae; aedeagus without numerous, serrated, minute processes. 6
- 6 Distal part of 10th sternite 1.9 times as wide as long; gonopods slightly triangular; distal part of aedeagus slightly rounded in ventral view.
- *S. melanocheilota* Chen & Chen, sp. n.
- Distal part of 10th sternite 1.7 times as wide as long; gonopods shovel-like, paramedially parallel but acute apically; distal part of aedeagus triangular in ventral view.
- *S. leucothorax* Chen & Chen, sp. n.
- 7 First flagellomere almost black; face black, yellow on lower margin; scutellum brown.
- *S. melanothorax* Chen & Chen, sp. n.
- First flagellomere yellow basally, black distally; face yellow, black on lower margin or corners; scutellum yellow. 8
- 8 Mesonotum yellow, with distinct dark brown stripes and patches laterally; fore femur with 6–7 setae on ventral surface; surstylus lacking prensiseta.
- *S. flaviscutellata* Chen & Chen, sp. n.
- Mesonotum yellow, without distinct dark brown stripes and patches laterally; fore femur with 3 setae on distal part of ventral surface. 9
- 9 Katapisternum dark brown; aedeagus with numerous, serrated, minute processes apically.
- *S. nigricypeata* Chen & Chen, sp. n.
- Katapisternum brown, slightly yellowish ventrally; aedeagus without serrated, minute processes
- *S. nigripalpata* Chen & Chen, sp. n.

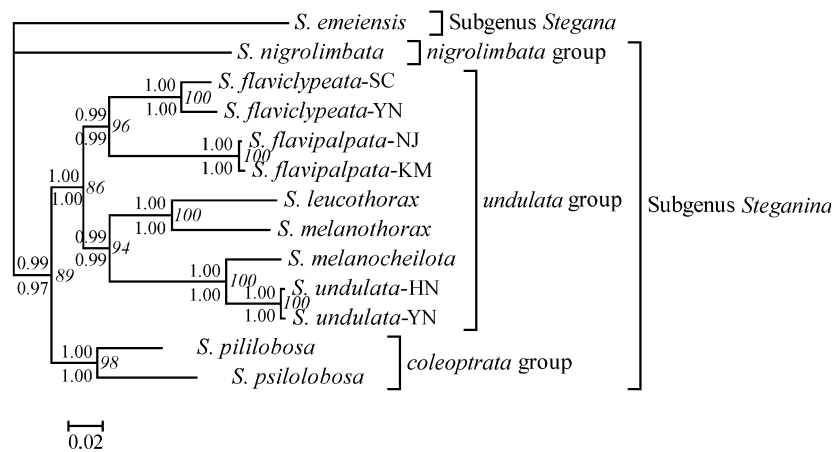


Fig. 45. Bayesian tree constructed using the concatenated sequences (2-partition scheme). Numbers above and below the branches indicate the posterior probabilities from 2- and 6-partition schemes, respectively; those to the right of the nodes (all shown in *italics*) are bootstrap percentages (1000 replicates) from the ME analysis.

MOLECULAR PHYLOGENY

Data summary

The alignment of the *ND2* sequences spans 1029 sites, with 210 parsimony informative (PI) out of 350 variable sites; the alignment of the *COI* sequences spans 710 sites, with 134 PI out of 182 variable sites. There are end gaps in the *ND2* sequences of *S. melanothorax* (sites 1–4) and *S. undulata*-YN (sites 1–11), and the *COI* sequences of *S. melanocheilota* (sites 1030–1043). Alignment gaps of three nucleotides were also found in the *ND2* sequences of *S. emeiensis* and *S. nigrolimbata* (both at sites 268–270).

The result of the tests using STATIO is shown in Table 2. The homogeneity was rejected for the partition of the 3rd codon position of the *ND2* sequences ($P = 0.24\%$) and all the *ND2*+*COI* sequences ($P = 3.14\%$). As shown in the same table, the test using DAMBE yielded *I*_{ss} indices significantly lower than the corresponding *I*_{ss}.*c* index for the concatenated sequences or each of the partitions for a symmetrical tree, and the the *I*_{ss}.*c* indices for an extreme asymmetric tree, except for the partition of the 3rd codon position of the *ND2*+*COI* sequences ($P = 0.3736$). Since none of the resultant trees in the present study are extremely asymmetric, there should be little substitution saturation in the sequences used in this study.

Phylogenetic reconstruction

The 2- and 6-partition Bayesian and the ME analyses yielded the same tree topology, therefore only the 2-partition tree is shown, with the node supports of each of the analyses shown on this tree. The monophyly of the *undulata* group was well-supported [bootstrap percentage (BP) in the ME analysis = 86; posterior probabilities (PPs) in the 2-/6-partition Bayesian analyses = 1.00/1.00] as was the *coleoptrata* group (BP = 98; PPs = 1.00/1.00). These two were sister groups (BP = 89; PPs = 0.99/0.97), while the three groups of the subgenus *Steganina* did not form a monophyletic assemblage with respect to the subgenus *Stegana*. Within the *undulata* group, *S. flaviclypeata* and *S. flavipalpata* formed a monophyletic

cluster (BP = 96; PPs = 0.99/0.99) and so did *S. leucothorax*, *S. melanothorax*, *S. melanocheilota* and *S. undulata* (BP = 94; PPs = 0.99/0.99). Within the latter cluster, two species pairs were recovered: *S. leucothorax* + *S. melanothorax* (BP = 100; PPs = 1.00/1.00) and *S. undulata* + *S. melanocheilota* (BP = 100; PPs = 1.00/1.00).

DISCUSSION

Base composition heterogeneity and phylogenetic relationship

It is critical in phylogenetic reconstruction to account for among-taxa base composition heterogeneity, because sequences of similar base compositions are prone to be clustered erroneously (Tarrío et al., 2001). In the present study, the base composition homogeneity was rejected in the STATIO test at either the 3rd codon position of the *ND2* sequences ($P = 0.24\%$) or the *ND2*+*COI* data set as a whole ($P = 3.14\%$). However, according to the results of this phylogenetic analyses, the base composition heterogeneity in the sequence data may be too limited to conceal the phylogenetic signals harboured in the sequences, since the phylogenetic analyses with either ME (taking into account the heterogeneous pattern among lineages) or Bayesian (not taking into account the heterogeneous pattern) methods recovered the same relationship among the taxa studied, and both methods yielded well-resolved relationships within the subgenus *Steganina*, except for the phylogenetic position of *S. nigrolimbata*.

Species delimitation

Meier et al. (2008) estimated the mean intraspecific variability, as well as the mean and smallest interspecific variabilities (%) of the mitochondrial *COI* sequences in Diptera. The estimates were $1.3\% \pm 1.6\%$, $10.1\% \pm 3.0\%$ and $5.9\% \pm 4.1\%$, respectively. In this study, the genetic distances between the *ND2* sequences of both *S. undulata* (0.002) and *S. flavipalpata* (0.005) are very small; the *COI* sequences of the Nanjian (NJ) and Kunming (KM) samples of *S. flavipalpata* are identical. These distances are below the lower limit of the interval of the smallest interspecific *COI* variability of Meier et al. (2008). This

corroborated the respective morphological similarities and strongly supports a conspecific status in both cases. As for *S. flaviclypeata*, a total of 30 or 25 nucleotide substitutions were found between the *ND2* or *COI* sequences of its Sichuan (SC) and Yunnan (YN) samples. The equivalent p-distances (0.029/0.035) are comparable to the upper limit of the mean intraspecific variability of mitochondrial *COI* sequence estimated by Meier et al. (2008), and falls in the estimate interval of the smallest interspecific variability. Actually, the p-distance of 0.029 in the *ND2* sequences is smaller than those among some very closely related *Drosophila* species (0.036–0.045), but larger than some intraspecific *ND2* sequence divergences in the genus *Paraleucophenga* (Zhao et al., 2009 and references therein). In this regard, the genetic distance between the two samples of *S. flaviclypeata* is likely to be of intraspecific level. However, the intra- and interspecific genetic distances may extensively overlap in Diptera (Meier et al., 2006), indicating that no universal cut-off criteria exist for determining the species status of dipteran species (DeSalle et al., 2005). Due to sparse taxon sampling at either the intra- or interspecific level in these molecular analyses, it is difficult to establish an objective threshold of distance for species diagnosis in the *undulata* group. In addition, currently there are only slight differences in the morphology recorded between the two local samples of *S. flaviclypeata*. Therefore, it may be premature to judge the significance of the differences between the samples of *S. flaviclypeata*.

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