A systematic study of *Ichneumonosoma* de Meijere, *Pelmatops* Enderlein, *Pseudopelmatops* Shiraki and *Soita* Walker (Diptera: Tephritidae)

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**Abstract**

Four fruit fly genera, *Ichneumonosoma* de Meijere, *Pelmatops* Enderlein, *Pseudopelmatops* Shiraki and *Soita* Walker, were studied and 19 species are recognized. Three new species, *Soita infuscata* Chen & Norrbom, *Ichneumonosoma quadrripunctata* Chen & Freidberg, and *I. triangularis* Chen & Norrbom are described and illustrated. *Ichneumonosoma* and *Soita* are revised, and keys to all the species are provided. *Ichneumonosoma imitans* (de Meijere) is newly recorded from Thailand. One new synonym is established: *Soita Walker* = *Xaniosternum* Enderlein, and *Xaniosternum ophioneum* Enderlein is moved from *Xaniosternum* to *Soita* (n. comb.). In addition, new morphological, geographic and biological information for two stalk-eyed fruit fly genera, *Pelmatops* and *Pseudopelmatops*, are provided. *Pelmatops fukienensis* Zia & Chen is newly recorded from Burma, *Pelmatops ichneumoneus* (Westwood) is newly recorded from Thailand and Burma, *Pseudopelmatops angustifasciatus* Zia & Chen is newly recorded from Vietnam, and the male of *P. angustifasciatus* is described and illustrated for the first time. The morphology of the compound eye and occipital protuberance of *Pelmatops* and *Pseudopelmatops* is described and illustrated for the first time. A cladistic analysis based on morphological characters of adults, a partial molecular analysis using the nuclear 28S rDNA (28S) and the mitochondrial cytochrome c oxidase I (COI) genes and a combined dataset were conducted to reconstruct the phylogeny of the four genera and their relationships amongst congeners, *Pelmatops* was well resolved; *Ichneumonosoma* and *Soita* were partly resolved, and *Pseudopelmatops* was unresolved. In addition, a hypothesis about the biology of *Pseudopelmatops* and its relationship with Sesidiæ (Lepidoptera) is discussed.

**Key words:** Tephritidae, *Ichneumonosoma*, *Pelmatops*, *Pseudopelmatops*, *Soita*, phylogeny, new species

**Introduction**

The fruit fly genera *Ichneumonosoma* de Meijere, *Pelmatops* Enderlein, *Pseudopelmatops* Shiraki and *Soita* Walker belong to the tribe Adramini of the subfamily Trypetinae. The species belonging to these genera are rather large (body length 8.8–16.0 mm), slender, wasp-like flies. They appear to be closely related to each other based on the following combination of characters, including ‘large size, male abdomen laterally compressed, metathoracic postcoxal bridge broadly sclerotised, femora without row of stout spinelike ventral setae’ (Hardy, 1983; Permkam and Hancock, 1995; Korneyev, 2000), which within Adramini is unique to the above four genera.
Here, we review all species of Ichneumonosoma and Soita, and provide new biological and geographic information for Pelmatops and Pseudopelmatops. Three new species, *S. infuscata* Chen & Norrbom, *I. quadripunctata* Chen & Freidberg, and *I. triangularis* Chen & Norrbom, are described and illustrated. To investigate phylogenetic relationships among the four genera and their species, especially the stalk-eyed fruit flies, *Pelmatops* and *Pseudopelmatops*, a cladistic analysis based on morphological characters of the adults, a partial molecular analysis using the nuclear gene 28S rDNA (28S) and the mitochondrial gene cytochrome c oxidase I (COI), and an analysis of a combined dataset were conducted. In addition, *Xaniosternum* Enderlein, 1920 is considered a synonym of *Soita* based on morphological comparison and phylogenetic analysis. A hypothesis about the biology of *Pseudopelmatops* species and their relationship with Sesiiidae (Lepidoptera) is proposed.

**Materials and methods**

**Taxonomic revision and morphology**

The studied material was obtained from the following collections, with their respective curators in parentheses:

AMS, Australia Museum, Sydney, Australia (David R. Britton); BAU, Beijing Agricultural University, Beijing, China (Ding Yang and Xin-li Wang); BMNH, The Natural History Museum, London, England, UK (Kim F.M. Goodger); BPBM, Bernice P. Bishop Museum, Honolulu, Hawaii, USA (Neal Evenhuis); CAS, California Academy of Sciences, San Francisco, USA (Charles E. Griswold); CNC, Canadian National Collection, Ottawa, Canada (Eduard Jendek); FFPRI, Forestry and Forest Products Research Institute, Kurokami, Kumamoto, Japan (Masahiro Sueyoshi); INHS, Illinois Natural History Survey, Champaign, Illinois, USA (Kathleen M. Methven); IPPE, Institute of Plant Physiology and Ecology, CAS, Shanghai, China (Jie Wu and Wei-bing Zhu); IZCAS, Institute of Zoology, Chinese Academy of Sciences, Beijing, China (Xiao-lin Chen); NAU, Northwest Agriculture & Forest University, Yangling, Shaanxi, China (Ying-lun Wang); OMNH, Osaka Museum of Natural History, Nagai Park, Higashi-sumiyoshi-ku, Osaka, Japan (Rikio Matsumoto); QMB, Queensland Museum, Brisbane (borrowed via AMS and BPBM); SMF, Senckenberg Museum, Frankfurt am Main, Germany (Damir Kovac); TAU, Tel Aviv University, Tel Aviv, Israel (Amnon Freidberg); USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C, USA (Allen Norrbom); ZMAN, Naturalis Biodiversity Center, Leiden (formerly Zoological Museum, Amsterdam), The Netherlands (Herman de Jong); ZMB, Museum für Naturkunde, Berlin, Germany (Joachim Ziegler).

Other abbreviations are used as follows: HT, holotype; LT, lectotype; ST, syntype.

The morphological terminology follows White et al. (1999) and McAlpine (1981). For the study of the male and female terminalia, the abdomen was detached from the body, cleared in a 10% KOH solution for 24 h or boiled for 5–10 minutes, neutralized in water and stored in glycerin; the terminalia were dissected from the abdomen, and observed in dorsal and lateral views under the microscope. Measurements are presented in millimeters.

**Phylogenetic analysis based on morphology**

A cladistic analysis was carried out with all species recognized in the taxonomic revision as the ingroup (Table S1). Specimens were examined of all species except *Pseudopelmatops nigricostalis* Shiraki, for which characters were scored from the literature (a few characters were scored for other species based on the literature, as detailed later).

Because the relationships among the genera of Adramini are not well resolved (Korneyev, 2000; Chen et al., 2006; Chen, unpublished data), and in order to obtain as broad conclusions as possible, the following five taxa were selected as the outgroup (Table S1). These are *Lenitovena trigona* (Matsumura), *Adrama apicalis* Shiraki, *Celidodacus fenestrata* (Enderlein), *Cyclopsia inscripta* (Walker) and *Euphranta camelliae* (Ito, 1949). Among them, *L. trigona* belongs to the Acanthonevrini, with the remainder belonging to the Adramini.

The data matrix used for the cladistic analysis contained 24 taxa and 27 adult morphological characters (Table S2). The phylogenetic analysis was performed using the parsimony software TNT (Goloboff et al 2008) and MrBayes ver. 3.2.3 (Ronquist & Huelsenbeck, 2003). In the TNT analysis, all characters were equally weighted and regarded as additive with Characters 4 and 25 scored by the 'step-matrix' option, and an exhaustive search using implicit enumeration (branch-and-bound) was performed. In the Bayesian analysis, all characters were regarded as unordered, with two Markov chain Monte Carlo (MCMC) analyses run for 10000 generations.
sampling trees every 10 generations, using four chains and a GTR+Gamma model. Convergence between the two runs was assessed using the average standard deviation of split frequencies (which ideally should be <0.01). The parameters were summarized discarding the first 25% as burnin.

TABLE S1. Ingroup and outgroup members used in cladistic analysis of Ichneumonosoma, Pelmatops, Pseudopelmatops and Soita (the examined specimen amount and depositories are given at end of each line).

<table>
<thead>
<tr>
<th>Ingroup</th>
<th>Outgroup</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ichneumonosoma consors (Walker, 1861)</td>
<td>Lenitovena trigona (Matsumura, 1905)</td>
</tr>
<tr>
<td>Ichneumonosoma heinrichi Hering, 1941</td>
<td>Adrama apicalis Shiraki, 1933</td>
</tr>
<tr>
<td>Ichneumonosoma imitans (de Meijere, 1911)</td>
<td>Conradiina fenestrata Enderlein, 1920</td>
</tr>
<tr>
<td>Ichneumonosoma quadripunctata Chen &amp; Freidberg, n. sp.</td>
<td>Cyclopsia inscripta (Walker, 1860)</td>
</tr>
<tr>
<td>Ichneumonosoma triangularis Chen &amp; Norrbom, n. sp.</td>
<td>Euphranta camelliae (Ito).</td>
</tr>
</tbody>
</table>

TABLE S2. Morphological Character matrix used in cladistic analysis for 24 taxa of Ichneumonosoma, Pelmatops, Pseudopelmatops, Soita and outgroup members.

<table>
<thead>
<tr>
<th>Character Code</th>
<th>0000000000</th>
<th>1111111111</th>
<th>22222222</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0123456789</td>
<td>0123456789</td>
<td>0123456</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Character</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>L. trigona</td>
<td>000001000</td>
</tr>
<tr>
<td>Ad. apicalis</td>
<td>0100100100</td>
</tr>
<tr>
<td>Co. fenestrata</td>
<td>000000110</td>
</tr>
<tr>
<td>Cy. inscripta</td>
<td>0100110100</td>
</tr>
<tr>
<td>E. camelliae</td>
<td>0000100100</td>
</tr>
<tr>
<td>I. consors</td>
<td>110012100</td>
</tr>
<tr>
<td>I. heinrichi</td>
<td>1100111000</td>
</tr>
<tr>
<td>I. imitans</td>
<td>1100121100</td>
</tr>
<tr>
<td>I. quadripunctata</td>
<td>1100121100</td>
</tr>
<tr>
<td>I. triangularis</td>
<td>1100321110</td>
</tr>
<tr>
<td>Pe. fukienensis</td>
<td>1001331002</td>
</tr>
</tbody>
</table>

...continued on the next page
Phylogenetic analysis based on the 28S and COI genes

Samples used for phylogenetic analysis were obtained either from pinned specimens or from specimens preserved in 95–100% ethanol. Detailed information on the sequenced specimens, including collection information, depositaries, DNA extraction numbers, the state of preservation and GenBank accession numbers are listed in Table S3. The morphological identification of previously undetermined specimens was performed mainly by the first author at the species/genus level with the aid of available keys and type material.

One leg was removed from each sampled specimen. Genomic DNA was extracted with a non-destructive method (without crushing the leg samples) using DNeasy Blood & Tissue Kit (Qiagen) following the manufacturer’s protocols.

DNA samples were amplified with 46 bp primers of 28S ribosomal RNA (rRNA) (Campbell et al., 1993) and a 52 bp primers of cytochrome c oxidase subunit I (COI) (Folmer et al., 1994).

PCR was performed in 25-μL reaction volumes. The final volume for 28S contained 12.5 μL 2 X PCR mix (Qiagen), 8.5 μL ddH₂O, 3.0 μL template DNA, and 0.5 μL (10 μM; Qiagen) of each primer. The final volume of COI contained 1 μL of template, 16.3 μL of water, 3.0 μL of buffer (10X conc., Qiagen), 1.5 μL of 25 mM of MgCl₂ (Qiagen), 1. 5 μL of each primer (5 μM, Operon Technologies), 1.0 μL of 10 mMdNTP mix (Promega) and 0.2 μL of Taq DNA polymerase (Qiagen) to complete the final volume of 25 μL.

PCR cycling conditions for amplification of the 28S fragment were 2 min at 94°C followed by 35 cycles of 1 min at 94°C, 45s at 58°C, 1min at 72°C. The COI gene fragment was amplified by 1 cycle of 3 min at 94°C followed by 39 cycles of 1 min at 94°C, 1 min at 50°C, 1 min at 72°C; and a final extension of 10 min at 72°C.

PCR products were checked by 1% agarose gel electrophoresis. Clearly amplified products were selected for sequencing. All those selected products were purified with ExoSAP-IT (USB Corp.) prior to sequencing. Purified PCR products were then sequenced using BigDye v3.1 on an ABI 3730xl DNA Analyzer (Applied Biosystems, Carlsbad, CA, USA). All sequences have been deposited in GenBank (see Table S3 for accession numbers).

DNA sequences of 28S and COI were aligned using ClustalW on MEGA v4.0 (Tamura et al., 2007). The phylogenetic trees were reconstructed based on the 28S and COI sequences by MEGA v4.0 and MrBayes ver. 3.2.3 (Ronquist & Huelsenbeck, 2003). The analysis was conducted in MEGA v4.0 under Maximum Parsimony (MP) methods; the percentage of replicate trees in which the sample specimens clustered together in the bootstrap test (1000 replicates) is shown as branch labels. For Bayesian analysis, a default setting model was performed, with other commands and options following morphology analysis.

Prior to this study, no molecular analysis of Ichneumonosoma, Pelmatops, Pseudopelmatops and Soita has been published, with no sequences publically available. All the molecular analyses were based on data generated during this study.
A comprehensive phylogenetic tree was reconstructed from the combined dataset of morphological characters, 28S and COI sequences. The mixed matrix was analyzed using MrBayes ver. 3.2.3 (Ronquist & Huelsenbeck, 2003), with two Markov chain Monte Carlo (MCMC) analyses run for 1,000,000 generations sampling trees every 1,000 generations, using four chains (GTR+Gamma model for the morphology data and GTR+Invgamma model for the molecular data). Convergence between the two runs was assessed using the average standard deviation of split frequencies (below 0.01). The parameters were summarized discarding the first 25% as burnin.

**Phylogenetic analysis based on the combined dataset of morphological characters, 28S and COI**

The biology of *Pseudopelmatops* and its possible relationship with *Sesiidae* (Lepidoptera)

The biology and behaviour of *Pseudopelmatops angustifasciatus* and *P. continentalis* Zia & Chen were observed on Tianmu Mountain, Zhejiang Province of China in the summer of 2013 by Yong Wang, a technician of the first author, and in the summer of 2014 by Yong Wang and the first author. A possible biological relationship of *Pseudopelmatops* with *Sesiidae* was tentatively suggested based on these observations and molecular evidence. The larvae of *Sesiidae* were identified by Prof. Chun-sheng Wu, an expert on Lepidoptera at the Institute of Zoology, Chinese Academy of Sciences. The related plant, *Rubus peltatus* Maxim., was identified by Mr. Min-shui Zhao, an expert of Tianmu Mountain Nature Reserve. The DNA extraction and molecular analyses of the 28S and COI genes of one Diptera larva found in the 'blocking cap' made by larvae of *Sesiidae* in *Rubus peltatus* followed the same methods used for the adult leg samples. The sequences of 28S and COI genes of this Diptera larva are provided in Table S4 and were included in the phylogenetic analysis.
TABLE S4. Sequences of 28S rRNA gene and cytochrome c oxidase subunit 1 (COI) genes from one Diptera larva found in the ‘blocking cap’ made by larvae of Sesiidae in summer of 2014, Tianmu Mountain, Zhejiang Province of China.

<table>
<thead>
<tr>
<th>DNA Region</th>
<th>Sequence (forward and reverse)5’→3’</th>
</tr>
</thead>
<tbody>
<tr>
<td>28S</td>
<td>AGCCCGATGAACCTGAATATCCATTATGAAAAATTCATCATTATACCGGATAATATTATATATTTATTATTATTAATATATTTGTGATAGTGTGCATTTTTTTCATATAAGGACATTGTGATCTATTAACATAATAAATAATTTATCAAAAAGATCATTAGCTTAAGTTTATTTGAATTAATTTGCTTTAAAAACATATTAACATAAAATAAATGCAAATGATTTGATAAAGTGTTGATAGATTTATTATATATAATGCTTAAATTGATTGAAATTTTACAATAATATTGAAATCCATGATTTTATATATTCATTGTATGCATTTATATGATTAACAATGCGAAAGATTCACGATACCTTCGGGACCCGTCT</td>
</tr>
<tr>
<td>COI</td>
<td>GCTCTAATTGGAGATGATCAAATTTATAATGTAATTGTTACGGCTCATGCTTTTGTAATAATTTTTTTTATAGTTATACCTATTATAATTGGAGGATTTGGTAATTGATTAGTACCTCTTATATTAGGAGCTCCAGATATAGCTTTCCCCTCGAATAAIAAXIAAGGTTCATTACCTCCCTCTCCTCCTACCTTATATTAAG1AAGAGAAGTAGAAATGGACCGGACAGGGACTGGTTAATACCCTCCTTTCTCTCTATATITGCTCAITGGAGAGCTTCGCTGA GACCTGCTATTTTTCTTCTTTACATTACCGTACGATACCTCCCTCTTTCTTCTTCTTCTTCTTCTTCTTCTTCTTCTTCTTCTT</td>
</tr>
</tbody>
</table>

Taxonomy

Key to genera of *Ichneumonosoma* de Meijere, *Pelmatops* Enderlein, *Pseudopelmatops* Shiraki and *Soita* Walker

1. Head strongly prolonged laterally, eyes at apices of long stalks (Figs. 57, 59, 63, 67–76, 79–82, 87–88) .......................... 2
   - Head normal in shape ................................................................................................................. 3
2. Orbital and genal setae absent; eye stalk in male rather long, longer than or about equal to length of abdomen (Figs.71–74); palpus spatulate, sparsely covered with fine, yellow setulae .......................... *Pelmatops* Enderlein
   - Orbital and genal setae present; eye stalk in male much shorter than abdomen (Figs. 81–82, 87–88 ); palpus narrow, parallel sided and densely covered with strong, black setulae ..................................... *Pseudopelmatops* Shiraki
3. Head with strong and strap-like orbital seta situated close to midlength of frons (Figs. 108–109, 125, 135–137); wing with entire vein R_{4+5}, and at least the base of vein Cu, covered with long, conspicuous setulae .......................... *Soita* Walker
   - Head with orbital setae weak or absent (Figs. 1–2, 8, 11, 17, 19, 26, 32, 34, 43, 51); wing with vein R_{4+5} setulose dorsally to beyond level of crossvein DM-Cu, but non-setulose distally, vein Cu, without setulae. ........... *Ichneumonosoma* de Meijere

*Ichneumonosoma* de Meijere


*Axania* Enderlein, 1920: 337. Type-species, *Axania ichneumonea* Enderlein (= *L.imitans* de Meijere), by original designation.

The genus *Ichneumonosoma* was proposed by de Meijere (1914) for a single species, *Lagarosia imitans* de Meijere, 1911 from Java, Indonesia. Hering (1941) added *I. heinrichi* from Sulawesi, Indonesia. Hardy (1983) referred this genus to the Euphrantini and provided a generic diagnosis plus diagnoses for *I. heinrichi* and *I. imitans*. Hardy (1986) subsequently referred this genus to the Adramini, transferred *Adrama consors* Walker to *Ichneumonosoma*, and provided a detailed generic diagnosis and a key to the three known species. Permkam and Hancock (1995) reviewed the diagnosis of this genus and newly recorded *I. consors* from Australia.

*Ichneumonosoma* is readily recognized by its very elongate abdomen and absence of many head and thoracic setae. It resembles *Soita* in having a sclerotized metathoracic postcoxal bridge and lacking postocular, genal, postpronotal, presutural supra-alar, acrostichal and katepisternal setae (Hardy, 1986). Other important characters include: head slightly broader than thorax in dorsal view; occiput convex, moderately swollen ventrally; face vertical or nearly so; antenna inserted at about middle of head in lateral view and slightly shorter than face; arista long plumose. Thorax lacking apical scutellar setae, wing with a short but distinct and pointed postdistal lobe on cell bcu, pterostigma subequal in length to cell c. Vein R_{4+5} setulose dorsally to beyond level of crossvein DM-Cu. Femora not spinose ventrally. Ocellar and dorsocentral setae absent. Lateral vertical seta present. Lateral scapular seta rudimentary.
This genus is poorly known and very rare in collections (Hardy, 1986). The host plants and biology are completely unknown. Here we describe *I. quadripunctata* Chen & Freidberg, n. sp. from Australia and *I. triangularis* Chen & Norrbom, n. sp. from Malaysia. The five currently known species are variously distributed in the Oriental (India, Thailand, Malaysia) and Australasian (Indonesia, Papua New Guinea, Australia) Regions.

**Key to the known species of Ichneumonosoma de Meijere**

1. Abdomen completely or almost completely yellow to yellow-brown, without narrow black bands on posterior margin of tergites 1–4; scutum with pair of rounded presutural black spots ......................................................... 2
   - Abdomen with narrow black bands on posterior margin of each of tergites 1–4; scutum with pair of large L-shaped presutural black marks .......................................................... 4
   2. Thorax only with pair of presutural black spots, other parts entirely yellow (Fig. 3). .................... *I. consors* (Walker)
   - Thorax in addition to presutural black spots, also with black spots on pleuron or postsuturally on scutum ................. 3
   3. Thorax with pair of short black postmarginal dorsocentral spots near transverse suture (possibly variable) (Fig. 13); anepisternum with large rounded dorsomedial black mark ............................................. *I. heinrichi* Hering
   - Thorax with pair of large round black spots near posterolateral corners of scutum; anepisternum without black markings (Fig. 37) ......................................................... *I. quadripunctata* Chen & Freidberg, n. sp.
   4. Head with round polished black spot over ocellar tubercle, dorsomedian portion of occiput and vertex, not extended anterolaterally to eye margin (Fig. 19); pleuron with separate large black marks on anepisternum, katepisternum and meron, and sometimes with small black mark on katatergite; orbital plate sparsely setulose .............................................. *I. imitans* (de Meijere)
   - Head with triangular polished black mark over ocellar tubercle, dorsomedian portion of occiput and vertex, extended anterolaterally to eye margin (Fig. 51); pleuron with black band on anepisternum only, katepisternum, meron, and katatergite without black markings; orbital plate finely but densely setulose ................................ *I. triangularis* Chen & Norrbom, n. sp.

**Ichneumonosoma consors** (Walker, 1861)
(Figs. 1–7)

*Adrama consors* Walker 1861: 296. Type locality: Indonesia, Maluku: Batchian [Bacan I.], (LT ♀ BMNH).


**Diagnosis.** Head with 1 frontal seta and with large polished oval black spot over ocellar tubercle and dorsomedian portion of occiput and vertex. Scutum with pair of oblong presutural black spots, without postsutural markings. Pleuron without black markings. Wing hyaline, with narrow fuscous costal band extending slightly beyond apex of vein R$_1$. No females were available for study, but according to Hardy (1986) and Permkan & Hancock (1995), the female ovipositor is rufous, conical, and as long as abdominal terga 3–6 combined; aculeus laterally compressed at tip, with median dorsal ridge bearing minute saw-like teeth, without distinct preapical setae.

**Description.** A large predominantly yellow to fulvous species (Figs. 4–5). Wing length 9.2 mm (the sex of the examined specimen is unknown because part of its abdomen is missing)

**Head** (Figs. 1–2). Completely yellow to fulvous except for an opaque black-brown mark on anterior median portion of frons and a large polished oval-shaped black spot over ocellar tubercle and dorsomedian portion of occiput and vertex. Head slightly broader than thorax in dorsal view and about as high as wide in lateral view. Frons about 2 times as long as wide and about as wide as eye in dorsal view. Antenna inserted at about middle of head in lateral view, slightly shorter than face; 1st flagellomere about 3 times as long as pedicel, 3 times as long as wide, apex rounded; arista short plumose. Occiput convex, distinctly swollen ventrally. Cephalic setae black: 1 frontal, 1 orbital, 1 medial vertical and 1 lateral vertical seta. Postocular and genal setae absent. Orbital plate non-setulose.

**Thorax** (Fig. 3). Completely yellow to fulvous except scutum with pair of oblong black presutural spots. Scutum slender, about twice as long as wide, with transverse suture complete and deep. Thoracic chaetotaxy: 2 (pairs) scapular, 1 dorsocentral, 1 scutellar, 2 notopleural, 1 postsutural supra-alar, 1 postalar, 1 intra-alar setae present; prescutellar acrostichal seta absent. Scutellar seta situated slightly closer to base than to apex. Wing (Figs. 6–7) hyaline, with narrow fuscous costal band extending from pterostigma to slightly beyond apex of vein R$_{4-5}$; cells bc and c colorless; veins R$_1$ and R$_{4-5}$ setulose dorsally, the latter to about level of crossvein DM-Cu; crossvein R-M situated at distal 1/3 of cell dm; cell bcu with posterodistal lobe short and broad, forming apical angle of approximately 45°. Legs completely yellow to fuscous; mid tibia with 1 large and 1 small black apicoventral spur.
Abdomen. Tergites 1–2 and anterior half of tergite 3 completely yellow-brown.

Distribution. Indonesia (Maluku), Papua New Guinea, Australia (Torres Strait Is.).


Host. Unknown.

**Ichneumonosoma heinrichi** Hering, 1941 (Figs. 8–16)


Diagnosis. Head with 2 frontal setae and small polished dark brown fan-shaped spot on vertex and anterior part of occiput. Scutum with pair of sublateral, rounded, posteriorly concave black spots anterior to transverse suture, and pair of short dark brown postdorsocentral vittae slightly posterior to transverse suture. Wing hyaline, with narrow fuscous costal band extending from pterostigma to apex of vein $R_{4+5}$ and slight infuscations over crossvein R-M and crossvein DM-Cu. Abdomen almost completely yellow-brown except for base of oviscape dark brown; oviscape about as long as abdominal tergites 5+6; aculeus laterally compressed at tip, with median dorsal and ventral ridges bearing distinct minute serrations, lacking preapical setae (tip of aculeus short triangular in lateral view, very acute in dorsal view).

Description. A large predominantly yellow to fulvous species (Figs. 9–10). Female: body length 15.0 mm; wing length 9.5 mm.

Head (Figs. 8, 11). Completely yellow to fulvous except for transverse ovoid opaque black mark on anterior median portion of frons and small polished dark brown fan-shaped spot over vertex and anterior part of occiput, narrowly connected to dark brown ocellar tubercle. Head slightly broader than thorax in dorsal view and about as high as wide in lateral view. Frons about 1.5 times as long as wide, and about as wide as eye in dorsal view. Antenna inserted at about middle of head in lateral view, slightly shorter than face; 1st flagellomere about 3 times as long as pedicel, 3 times as long as wide, apex rounded; arista short plumose. Occiput convex, distinctly swollen ventrally. Cephalic setae black: 2 frontal, 1 orbital, 1 medial vertical and 1 lateral vertical setae. Postocellar and genal setae absent. Orbital plate non-setulose.

Thorax (Fig. 13). Completely yellow to fulvous except scutum with pair of sublateral rounded, posteriorly concave black presutural spots, and pair of short dark brown postdorsocentral vittae; and anepisternum with 1 ovoid black mark posterodorsally. Scutum slender, about twice as long as wide, with transverse suture complete and deep. Thoracic chaetotaxy: 2 scapular, 1 dorsocentral, 1 scutellar, 1 postpronotal, 2 notopleural, 1 poststernal supra-alar, 1 postalar, 1 intra-alar, and 1 anepisternal setae present; prescutellar acrostichal setae absent. Scutellar setae situated closer to base than to apex. Wing (Fig. 12) hyaline, with narrow fuscous costal band extending from pterostigma to apex of vein $R_{4+5}$ and slight infuscations over crossvein R-M and crossvein DM-Cu; cells bc and c hyaline; veins $R_3$ and $R_{4+5}$ setose dorsally, the latter to beyond level of crossvein DM-Cu; crossvein R-M situated beyond middle of cell dm; cell bcu with posterodiscal lobe short and broad, forming angle of less than 45°. Legs entirely yellow to fuscous; mid tibia with 1 large and 1 small black apicoventral spurs.

Abdomen. Almost completely yellow-brown except for base of oviscape dark brown. Tergites 3 and 4 about same length, and tergite 5 slightly shorter than tergite 4; oviscape cylindrical, as long as abdominal tergites 5+6. Aculeus (Figs. 14–16) laterally compressed at tip, with median dorsal and ventral ridges bearing distinct minute serrations, lacking preapical setae (tip of aculeus short triangular in lateral view, very acute in dorsal view).

Distribution. Indonesia (Sulawesi).

Specimen examined: INDONESIA: Sulawesi: S. Celebes Talassa (Maros), 300m, October 1931, G. Heinrich. Holotype ♀ (ZMB).

Ichneumonomosoma imitans (de Meijere, 1911)
(Figs. 17–24; 25–30)

Axania ichneumonea Enderlein 1920: 338. Type locality: India. Sikkim. (ST both sexes ZMB, BMNH).

Diagnosis. Head with 1 frontal seta, 3–4 medial vertical setae and large polished round black spot over ocellar tubercle and dorsmedian portion of occiput and vertex. Scutum with pair of large somewhat L-shaped black marks presuturally and 2 large somewhat inverted J-shaped black marks poststurally. Wing almost completely hyaline, with narrow fuscous costal band extending from perostigma to slightly beyond apex of vein $R_{4+5}$ and slight infuscation over crossvein R-M. Abdomen yellow to yellow-brown, with narrow black bands on posterior margin of each of tergites 1–6 in female and 1–4 in male.

Description. A large predominantly yellow to fulvous species. Female. Body length 10.7 mm, wing length 8.2 mm.; Male. Body length 11.2 mm; wing length 10.2 mm.

Head (Fig. 19). Completely yellow to fulvous except for triangular opaque black mark on anterior median
portion of frons and large polished round black spot over ocellar tubercle and dorsomedian portion of occiput and vertex. Head slightly broader than thorax in dorsal view and slightly higher than wide in lateral view. Frons about 1.5 times as long as wide, and about as wide as eye in dorsal view. Antenna inserted at about middle of head in lateral view, slightly shorter than face; 1st flagellomere about 3 times as long as pedicel, 3 times as long as wide, apex rounded; arista short plumose. Occiput convex, distinctly swollen ventrally. Cephalic setae black: 1 frontal, 1 orbital, 3 medial vertical and 1 lateral vertical setae. Postocellar and genal setae absent. Orbital plate sparsely setulose.

Thorax (Fig. 22). Predominantly yellow to fulvous except for following black areas: scutum with pair of large, somewhat L-shaped presutural marks composed of submedial vitta and band along anterior margin of transverse suture and pair of large, somewhat inverted J-shaped postsutural marks (composed of submedial spot connected to

dorsocentral vitta and band on posterior scutal margin); anepisternum with large medial band, katepisternum with oblique medial band, and meron mostly black; mediadcter with pair of broad black vitta; katatergite sometimes with small spot. Scutum about 1.6 times as long as wide, with transverse suture complete and deep. Thoracic chaetotaxy: 2 pairs of scapular, 1 dorsocentral, 1 scutellar, 1 postprontal, 2 notopleural, 1 postsutural supra-alar, 1 postalar, 1 intra-alar, 1 anepisternal, and 1 anepimeral setae present; prescutellar acrostichal seta absent. Scutellar seta situated closer to apex than to base. Wing (Fig. 24) almost completely hyaline, with narrow fuscous costal band extending from pterostigma to slightly beyond apex of vein R_{4+5} and slight infuscation over crossvein R-M; cells bc and c colorless; veins R_1 and R_{4+5} setulose dorsally, the latter to slightly beyond level of crossvein DM-Cu; crossvein R-M situated beyond middle of cell dm; cell bc with posterodistal lobe short and broad, forming angle less than 45°. Legs predominantly yellow to fuscous except for mid and hind femur basally dark brown, and hind tibia with basal half dark brown; mid tibia with 2 large black apicoventral spurs.


Abdomen (Figs. 18, 20). Female: Abdomen yellow to yellow-brown, with narrow black band on posterior margin of each of tergites 3–6, subbasal inverted-U shaped mark plus band on posterior margin of syntegrite 1+2.
Tergites 3, 4 and 5 about same length. Oviscape cylindrical, about as long as abdominal tergites 5+6; aculeus (Fig. 21, 23) laterally compressed at tip, with median dorsal ridge bearing distinct minute serrations, lacking preapical setae (tip of aculeus blunt in lateral view, very acute in dorsal view). Male: Abdomen yellow to yellow-brown, with narrow black bands on posterior margin of each of tergites 3–4, subbasal inverted-U shaped mark plus band on posterior margin of syntergite 1+2, and elongate black median mark on posterior half of tergite 5.

**Distribution.** India (Sikkim), Thailand (Mae Hong Son; new country record), Malaysia (Peninsular Malaysia, Negri Sembilan), Indonesia (Java).


**Ichneumonosoma quadripunctata** Chen & Freidberg, new species (Figs. 31–40)

**Diagnosis.** Head with 1 frontal seta and polished black triangular mark over ocellar tubercle and dorsomedian portion of occiput and vertex. Scutum with 2 pairs of large round sublateral dark spots, one just presuturally and one just anterior to scutoscutellar suture. Anepisternum without brown markings. Wing nearly completely hyaline, with narrow fuscous costal band extending from pterostigma to beyond apex of vein R.

**Description.** A large predominantly yellow species (Figs. 31, 38). Female: body length 11.0 mm; wing length 7.6 mm.

Head (Figs. 32, 34). Completely yellow to fulvous except for nearly rectangular opaque black mark on anterior median portion of frons, large polished black anteriorly acute, posteriorly rounded subtriangular spot over ocellar tubercle and dorsomedian portion of occiput and vertex. Head broader than thorax in dorsal view and slightly higher than wide in lateral view. Frons about 1.5 times as long as wide, and about as wide as eye in dorsal view. Antenna slightly shorter than face; 1st flagellomere about 3 times as long as pedicel, 3 times as long as wide, apex rounded; arista short plumose. Occiput convex, distinctly swollen ventrally. Head setae black: 1 frontal, 1 postsutural supra-alar, 1 postalar, 1 intra-alar lateral vertical setae.

Thorax (Fig. 37). Mostly yellow except scutum with pair of large round black presutural sublateral spots and similar, slightly smaller black sublateral spots near posterior margin. Scutum slender, about 1.8 times as long as wide, with transverse suture complete and deep. Thoracic chaetotaxy: 2 pairs scapular, 1 dorsocentral, 1 scutellar, 2 notopleural, 1 postsutural supra-alar, 1 postalar, 1 intra-alar setae present; prescutellar acrostichal setae absent. Scutellar seta situated slightly closer to base than to apex of scutellum. Wing (Figs. 35, 36) almost completely hyaline, with narrow fuscous costal band extending from pterostigma to beyond apex of vein R.

Legs completely yellow; mid tibia with 1 large and 1 small black apicoventral spur.

Abdomen. Yellow to yellow-brown, but with 1 medial irregular dark-brown mark on tergites 1+2 and 2 lateral irregular dark-brown marks on tergites 4–5. Oviscape cylindrical, slightly longer than length of tergites 5+6; aculeus (Figs. 33, 39, 40) laterally compressed at tip, with median dorsal and ventral ridges bearing distinct and minute serrations, lacking preapical setae (tip of aculeus short triangular in lateral view, very acute in dorsal view).

**Distribution.** Australia (northern Queensland).

**Type data:** Holotype ♀ (QMB), AUSTRALIA: Cairns, N Qld, 24–30 December 1967, G. Monteith.

**Etymology.** The name of this species is an adjective in reference to the 4 spots on the scutum.

**Remarks.** This species is similar to *I. heinrichi*, which differs by lacking the pair of large round black spots near the posterior margin of the scutum, having a black mark on anepisternum, abdomen without irregular dark-brown marks, and head with 2 frontal setae. This species is also similar to *I. consors*, which also differs by lacking the pair of postsutural round black spots on the scutum and 1 medial irregular dark brown mark on syntergite 1+2, and cell bcu of wing with posterodistal lobe less acute.
ICHNEUMONOSOMA TRIANGULARIS CHEN & NORRBOM, NEW SPECIES
(Figs. 41–48; 49–56)


Diagnosis. Head with 1 frontal seta and large polished triangular black mark over ocellar tubercle and dorsomedian
portion of occiput and vertex extended anterolaterally to eye margin. Scutum with pair of large, somewhat L-shaped presutural black marks; pair of large somewhat inverted J-shaped postsutural black marks. Wing almost completely hyaline, with narrow fuscous costal band extending beyond vein R$_{4+5}$ and slight infuscations over crossvein R-M and crossvein DM-Cu. Abdomen yellow to yellow-brown, with narrow black bands on posterior margin of each of syntergite 1+2 and tergites 3–6 in female, and syntergite 1+2 and tergites 3–4 in male.

**FIGURES 41–48 Ichneumonosoma triangularis** (Female) 41. Habitus, dorsal view; 42. Habitus, lateral view; 43. Head and thorax, lateral view; 44. Abdomen, dorsal view; 45. Scutum, dorsal view; 46. Abdomen, lateral view; 47. Aculeus, dorsal view; 48. Tip of aculeus, lateral view.

**Description.** A large predominantly yellow to fulvous species. Female (Figs. 41, 42): body length 12.2 mm; wing length 8.9 mm. Male (Figs 49, 50): body length 12.3 mm; wing length 9.8 mm.

Head (Fig. 51.). Completely yellow to fulvous except large opaque triangular black mark on anterior median portion of frons, large polished triangular black mark over ocellar tubercle and dorsomedian portion of occiput and
vertex, extended anterolaterally to eye margin, and antennae dark brown. Head slightly broader than thorax in dorsal view and distinctly higher than wide in lateral view. Orbital plates with dense fine setulae. Frons about 1.3–1.5 times as long as wide, and about as wide as eye in dorsal view. Antenna slightly shorter than face; 1st flagellomere about 3 times as long as pedicel, 3 times as long as wide, apex rounded; arista short plumose. Occiput convex, distinctly swollen ventrally. Head setae black: 1 frontal and 1 lateral vertical setae. Orbital, medial vertical, postocellar and genal setae absent. Dorsal 1/3 of frons with numerous fine black setulae.

**FIGURES 49–56 Ichneumonosoma triangularis** (Male) 49. Habitus, dorsal view; 50. Habitus, lateral view; 51. head, dorsal view; 52. Wing; 53. Abdomen, dorsal view; 54. Head and thorax, lateral view; 55. Terminalia, lateral view; 56. Terminalia, posterior view.

Thorax (Fig. 45). Predominantly yellow to fulvous except for following black marks: pair of large somewhat L-shaped presutural scutal marks (composed of submedial vitta and band along anterior margin of transverse suture); and pair of large, somewhat inverted J-shaped postsutural marks (composed of submedial spot connected to dorsocentral vitta and band on posterior scutal margin); pair of large somewhat J-shaped postsutural scutal marks; 1 broad band on anepisternum; and 2 broad vittae on mediotergite. Scutum about 1.5–1.6 times as long as wide, with transverse suture complete and deep. Thoracic chaetotaxy: 2 pairs scapular, 1 dorsocentral, 1 scutellar, 1 postpronotal, 2 notopleural, 1 postsutural supra-alar, 1 postalar, 1 intra-alar, 1 anepisternal, 1 anepimeral setae present; prescutellar acrostichal seta absent. Scutellar seta situated closer to apex than to base of scutellum. Wing (Fig. 52) almost completely hyaline, with narrow fuscous costal band extending from pterostigma to beyond apex of vein R_{4+5} and slight infuscations over crossvein R-M and crossvein DM-Cu; cells bc and c hyaline; veins R, and
R₄+₅ setulose dorsally, the latter distinctly beyond level of crossvein DM-Cu; crossvein R-M situated beyond middle of cell dm; cell bcu with posterodistal lobe short and broad, forming angle of approximately 45º. Legs predominantly yellow to fuscous except mid and hind femora with basal part dark brown, hind tibia with basal half dark brown; mid tibia with 2 large black apicoventral spurs. All femora, tibiae and tarsi covered with numerous black short fine hairs except for fore femur.

Abdomen. Female (Figs 44, 46): Abdomen yellow to yellow-brown, with narrow black bands on posterior margin of each of syntergite 1+2 and tergites 3–6, and 2 narrow lateral black bands at sides of tergite 2. Tergites 3, 4 and 5 about same length. Oviscape cylindrical, about as long as tergites 5+6; aculeus laterally compressed at tip, with median dorsal and ventral ridge bearing distinct serrations, lacking preapical setae (tip of aculeus triangular in lateral view, very acute in dorsal view). Male (Fig. 53): Abdomen yellow to yellow-brown, with narrow black bands on posterior margin of each of syntergite 1+2 and tergites 3–4, and a narrow longitudinal black band at middle of tergite 5.

**Distribution**: Malaysia (Kuala Lumpur).


**Etymology**: The name of this species is an adjective in reference to the triangular black mark dorsally on the head.

**Remarks**: This species is similar to *I. imitans*, differing by the triangular shape of the black mark over the ocellar tubercle and dorsomedian portion of the occiput and vertex which extend anterolaterally to the eye margin, the orbital plates with dense fine setulae, and the katepisternum and meron lacking black markings. The holotype was illustrated (as *I. imitans*) by Hancock & Drew (1995, fig. 11).

**Pelmatops** Enderlein, 1912

Enderlein (1912) proposed *Pelmatops* for a single species, *Achias ichneumoneus* Westwood, 1850, from India. Zia & Chen (1954) added *P. fukienensis* from Fujian, China. Chen et al (2010) revised the genus, added a new species, *P. tangliangi*, from China, India and Vietnam, and provided a key. In recent years, new information on the distribution and biology has been accumulated. The northernmost extent of the distribution of the genus is now known to be Shaanxi Province in central China. Detailed ecological data for *P. ichneumoneus* (from Yunnan, China) and *P. tangliangi* (from Tam Dao, Vietnam) were recorded and analyzed, and the behaviour of these two species in the field was observed and recorded for the first time. In summary, *Pelmatops* includes three species, with known distribution in the Oriental Region (southern China, India, Vietnam, and Nepal) and the Oriental-Palaearctic transition zone (central China).

**Pelmatops fukienensis** Zia & Chen, 1954

(Figs. 57–62, 89, 98)


**Description** (supplement to the species description of Chen et al, 2010). Compound eye wholly smooth and rounded, without projection; ommatidia similar in size (Fig. 89). Occipital protuberance in female flat, rectangular, not clearly delimited from occiput, setae on its posterior margin short and numerous (Fig. 98). Male terminalia: epandrium large and broad in posterior view; lateral surstylus small and short, apex rounded in lateral view; medial surstylus with 1 black prensiseta (Fig. 61).

**Distribution**: China (Fujian, Sichuan, Shaanxi (new record), Taiwan), Burma (new record).

**Specimens examined**. BURMA: Chin Hills, Mt Victoria, 2400–2800m, May 1938, G. Heinrich, 2♀ (BMNH, checked by D.L.Hancock, pers. comm.); CHINA: Fujian: Chongan, 750 m, 24 June 1960, Y. R. Cheng, 1♀ (IZCAS); Shaowu, 20 April 1943, C.C. Maa, HT ♂ (IZCAS, head missing, male genitalia are shown in Fig. 61), 1 PT♀ (IZCAS). Sichuan: Mt. Emei, 21 July 1957, K.R. Huang; 26 May 1957, L.Y. Zheng, 2♀ (IZCAS). Taiwan:

**Remarks.** The record from Shaanxi extends the known distribution of *Pelmatops* northward to the Oriental-Palearctic transition zone, and that from Burma extends the known southern limit of the range.

**FIGURES 57–62** *Pelmatops fukienensis* 57. Head and Thorax, lateral view (female); 58. Head, dorsal view (female); 59. Habitus, dorsal view (female); 60. Aculeus, dorsal view (female); 61. Genitalia, lateral posterior view (male); 62. Abdomen, dorsal view (female).
**Pelmatops ichneumoneus** (Westwood)  
(Figs. 63–66; 67–70; 90–91, 100–101)


**Description** (supplement to the species description of Chen et al, 2010). Compound eye entirely smooth and rounded, without projection in female (Fig. 90), but with rounded projection in male (Fig. 91); ommatidia similar in size. Occipital protuberance flat, rectangular, not clearly delimited from occiput, setae on its posterior margin short and sparse in female (Fig. 100), but medium-sized and numerous in male (Fig. 101).

**Distribution.** China (Sichuan, Yunnan, Xizang, Hainan), India, Nepal, Burma (new record), Thailand (new record).

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**FIGURES 63–66 Pelmatops Ichneumoneus**  
63. Habitus (female), photo taken in field cage in Yunnan, China; 64. Collecting site in Yunnan, China, showing the ground layer vegetation; 65. Collecting site in Yunnan, China, showing the canopy vegetation; 66. Collecting site in Yunnan, China, showing understory vegetation. (by Yong Wang).

Biology. The flies and their collection sites were observed and photographed in Benggang, Yunnan Province, China (Figs. 63–66) by Yong Wang in summer of 2013. The collecting site had an average temperature of about 20°C during the day with very high humidity and strong fog. The collecting site had flourishing plants (Figs. 64–66), including tall trees and shrubs covered with numerous thorny vines and a large variety of flowers and fruits. In the top of the canopy, the foliage was very dense (Fig. 65). One individual of *P. ichneumoneus* in this site has been collected and reared in a cage outside the collecting site for several days (Fig. 63). An adult fly was also observed and photographed in Kamphaeng Phet Province, Thailand (Figs. 67–70) by Sorasak Nak-iam, a PhD student in Naresuan University of Thailand, in the summer of 2012. According to his observations, the site was an evergreen forest where a fly was found on an undergrowth leaf. The fly was observed flying slowly, and it was the first time that this species was found resting on moss (Figs. 67–68).

**FIGURES** 67–70 *Pelmatops ichneumoneus* Habitats (female), photos taken in Kamphaeng Phet, Thailand (by Sorasak Nak-iam).
Pelmatops tangliangi Chen, 2010
(Figs. 71–74; 92, 99)

Pelmatops tangliangi Chen, in Chen et al., 2010:3. Type–locality: Benggang, Menghai, Yunnan, China (HT ♂ IZCAS).

Description (supplement to the species description of Chen et al., 2010). Compound eye smooth and round, with sharp projection at end in male; ommatidia different in size, those located on projection slightly larger (Fig. 92). Occipital protuberance of male flat, rectangular, not clearly delimited from occiput, setae on its posterior margin medium-sized and numerous (Fig. 99).

Distribution. China (Yunnan), India, Vietnam.

Specimens examined. CHINA: Yunnan: Xishuangbanna 1750m, November 2008, J. Hu & L. Tang, 1 HT ♂ (IZCAS). INDIA: Ranikhet, June 1949, I. M. Newell, 1 PT ♂ (BPBM); Khasi Hills, Assam, purchased from E. Heyne, 97–82, 1♂, 1♀ (BMNH, checked by D.L. Hancock, pers. comm.). VIETNAM: Vinh Phu Prov.: Tam Dao, 500–1000m, 2 June 1997, R. Matsumoto, 1 PT ♂ (OMNH); Tam Dao, 1200m, 13–14 May 2012, Eduard Jendek, 2♂ (CNC, examined by photos and videos, which taken by Eduard Jendek and sent to the first author).

Biology. Eduard Jendek, a Canadian entomologist working in the Ottawa Plant Laboratory, Canadian Food Inspection Agency, observed and took photos (Figs. 71–74) and videos of this species in Vietnam in the summer of 2012. According to him, three of the individuals occurred in a small area (6 square meters) at the side of a jungle trail, close to the margin with an open space. The flies were flying relatively slowly and were cumbersome. The first author visited the type locality of this species in Yunnan, China in autumn of 2012, and found this site to be very similar to the site which was described above for *P. ichneumoneus* in landscape, vegetation, humidity and temperature.

**FIGURES 71–74 Pelmatops tangliangi** Habitus (males) in field in Vietnam (photos taken by Eduard Jendek and sent to first author for identification).

**Pseudopelmatops Shiraki**

*Pseudopelmatops* Shiraki, 1933: 49. Type-species: *P. nigricostalis* Shiraki, 1933, by original designation.

*Pseudopelmatops* was proposed by Shiraki (1933) for a single species, *P. nigricostalis* from Taiwan, China. Zia &
Chen (1954) added two species from Zhejiang, China, *P. angustifasciatus* and *P. continentalis*. Chen et al (2010) revised this genus, added two more species, *P. indiaensis* Chen from India and *P. yunnanensis* Chen from China, and provided a key. In subsequent years, some new information on its distribution and biology has accumulated. The northernmost distribution of the genus is now known to extend to Shaanxi and Henan Provinces in central China which is regarded as the Oriental-Palearctic transition zone. Detailed environmental conditions at the collection sites of *P. angustifasciatus* and *P. continentalis* are also reported here and analyzed, and observations of the behaviour of these species in the field are recorded for the first time. In addition, *P. angustifasciatus* is first recorded from Vietnam, and the male is associated with the female by mating behaviour and described for the first time. Moreover, we provide supplemental morphological information for *P. angustifasciatus*, *P. continentalis*, *P. indiaensis* and *P. yunnanensis*.

**Biology of Pseudopelmatops species and their possible relationship with Sesiidae (Lepidoptera)**

Xiao-lin Chen and Yong Wang observed the biology and behaviour of *Pseudopelmatops angustifasciatus* and *P. continentalis* in the field at Tianmushan, Zhejiang Province in the summer of 2013 and 2014. We often found adults of these two species on or near a ‘blocking cap’ (Fig. 157) outside the openings of mines made by larvae of Sesiidae (Fig. 159) in stems of *Rubus peltatus* Maxim. (Rosaceae). The flies spent long time on or near these caps. We observed a male of *P. angustifasciatus* even staying there for one day and night (Figs. 160, 161). We also observed interaction between a male and female of *P. angustifasciatus* beside one ‘blocking cap’ (Figs. 162, 163), but mating or oviposition were not observed. Two Diptera larvae were found in one ‘blocking cap’ (Fig. 156). We extracted DNA and partially sequenced the 28S and COI genes from one larva, then carried out molecular analysis with the adult data. The results of the 28S (Table S4, Fig. 154) and COI (Table S4, Fig. 155) analyses grouped this larva with *Pseudopelmatops* adults, although they did not resolve whether it is conspecific with either *P. angustifasciatus* or *P. continentalis*.

Several open puparia morphologically similar to that of Soita also were discovered in the lower part of stem mines that extended to the roots of *R. peltatus* (Fig. 166, 167) in the early spring and winter of 2014. We highly suspect that these puparia are one or more species of Pseudopelmatops. To guide our future study of the biology of Pseudopelmatops, we hypothesize that in summer or early autumn, the female of Pseudopelmatops might lay eggs in the ‘blocking cap’, and the eggs hatched into larvae there. As the larvae develop (perhaps as second or third instars), they may enter the mine and bore deeper, eventually reaching the root of *R. peltatus* where they pupate and overwinter.

**Pseudopelmatops angustifasciatus Zia & Chen, 1954**

(Figs. 75–86; 93–94, 97,102–103 )


**Description Female**

(supplement to the species description of Chen et al, 2010). Compound eye somewhat rough and rounded, with 2 shapes in female, one lacking projection (Fig. 93), the other with small projection (Fig. 94); ommatidia similar in size. Occipital protuberance in female inverted trapezoidal in shape, and somewhat bifid, distinctly delimited from occiput, setae on posterior margin long and sparse (Fig. 102).

**Male** (described for first time). Body length 12.0 mm; wing length 9.6 mm. The body predominantly dark brown to black and subshining (Figs. 81–82). Head (Figs. 79–80): Dark brown to black except for middle of frons yellow, ventral part of face, parafacial and palpus yellow to yellow-brown. Palpus narrow, parallel-sided and densely covered with strong, black setulae. Chaetotaxy reduced: head with orbital, medial vertical and genal setae present; postocellar, lateral vertical, ocellar and frontal setae absent. Antenna almost equal to face, with 1st flagellomere about 1/4 as wide as long; arista plumose, longest ray slightly shorter or about equal to width of 1st flagellomere. Compound eye rounded, with small projection, and distinct linear green reflection area at dorsal 1/3; ommatidia about same size (Fig. 97). Occiput protuberance inverted trapezoidal and somewhat bifid, setae on its posterior margin long and sparse, with distinct border with occiput (Fig. 103). Thorax (Fig. 84) entirely dark brown to black, halter white. Chaetotaxy reduced: only 1 posterior notopleural, 1 postalar and 1 apical scutellar setae present. Wing (Fig. 85). Largely hyaline with a narrow brownish black band extending from crossvein R-M to

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costal margin in middle of cell r
er, then along costa to wing apex, also with pale, very slender, and sometimes interrupted basal extension into cells dm and cu₁; also with anteromedial mark, orange in pterostigma, brown in area of cell r₁, posterior to pterostigma and in extreme base of cell r₂+₃, pterostigma narrow and long, about 0.98 times as long as cell c. Vein R₄+₅ bare. Legs slender and long. Coxae, trochanters and basal 2/3 of femora dark brown, other parts yellow-brown. Abdomen elongate with tergites 1–2 black, tergites 3–4 dark brown, and tergite 5 yellow except medially; tergites 1–2 nearly parallel-sided and almost equal to combined length of tergites 3 and 4. Male terminalia (Fig. 86): Epandrium large and broad, rounded in posterior view; lateral surstylus small and short, apex rounded; medial surstylus with 1 black prensiseta.

**Distribution.** China (Hubei, Hunan, Zhejiang, Fujian, Sichuan, Guizhou, Yunnan), Vietnam (new record). Yunnan is a new province record.

**FIGURES 75–78** *Pseudopelmatops angustifasciatus* 75. Habitus (female) in Zhejiang, China 76. A male and female mating in cage in summer of 2014; 77. *Rubus peltatus* at collecting site in Zhejiang, China in summer; 78. Same, in winter. (by Yong Wang and Xiao-lin Chen).

**Specimens examined.** CHINA: Fujian: Shaowu, 20 April 1942, 1♀ PT; Shaowu, 900–1170 m, 28 May 1960, Y. R. Zhang, 1♀. Guizhou: Xishui, 800m, 24–28 September 2000, W. Xiao, 1♀; Kuankuoshui natural reserve, SonglinYakou, 7–8 August 2013, in yellow trap, 1♀. Hubei: Badong, 1500m, 14 July 2006, Y. L. Chen, 1♀;
Hefeng, 1400 m, 31 July 1989, S. Y. Wang, 1♀. Hunan: Liuyang, Daweishan, 1200m, 8 August 2012, W. Xiao, 1♀; Tianpingshan, 18 August 1981, 1♀. Sichuan: Mt. Emei, May–July 1957, K. R. Huang, 2♀; Mt. Wawu, 1750m, N29.40.031 E102.56.498, 11 August 2007, F. Liu, 1♀. Yunnan: Xishuangbanna, Menghai, Benggang, 27 August 2013, Y. Wang & C. Wang, 1♀. Zhejiang: Tianmushan, 13 July 1937, 1♀ LT; Tianmushan, 8 July 1936, 1♀ PT; Tianmushan, 25 July 1937, 1♀ PT; Tianmushan, Xianrrending, 1500m, 14–30 June 2013, Y. Wang & F. Yuan, 8♀; Tianmushan, Xianrrending, 1500m, 8 July 2014, Y. Wang, 1♀; Tianmushan, Xianrrending, 1500m, 29–30 June 2013, Y. Wang, in yellow trap, 1♂; Tianmushan, Xianrrending, 1500m, 8 July 2014, Y. Wang, 1♂; Tianmushan, 26 June 1961, E. Suenson, 1♀ (USNM). VIETNAM: Sapa, Huanglianshan, 1826m, 22 August 2013, X.L. Chen, Y. Wang and C. Wang, 1♀. All material deposited in IZCAS except for that mark ‘USNM’.

FIGURES 79–86 Pseudopelmatops angustifasciatus (Male) 79. Head, lateral view; 80. head, dorsal view; 81. Habitus, lateral view; 82. Habitus, dorsal view; 83. Abdomen, dorsal view; 84. Scutum, dorsal view; 85. Wing; 86. Terminalia, ventral view.
**Biology.** The biology and behaviour of this species were observed on Tianmu Mountain, Zhejiang Province, China in the summer of 2013 by Yong Wang, and in the summer of 2014 by Yong Wang and the first author. In summer, the forest was partially shaded, and the temperature was 25–30°C during the day and 15–20° at night. However, there was very high humidity at night and the dew on the leaves usually did not dry until the next noon. The collecting site had two different kinds of vegetation: the canopy was comprised of tall trees with sparse leaves, seldom with flowers and fruits; the dominant plant of the understory was *Rubus peltatus* Maxim. (Rosaceae), a deciduous shrub that is mainly distributed in China. *Rubus peltatus* can grow 1–2 m high (Fig. 77), and it has a thick stem and roots that were still living in winter (Fig. 78).

The living individuals of *P. angustifasciatus* observed in Zhejiang usually were alert and agile, escaped quickly from people 2–3 m away; but remained still if the observers did not move. The majority of individuals of *P. angustifasciatus* were observed resting on *R. peltatus*, and they usually walked on both the top and underside of the leaves, also on stems, and often waved their wings. Because individuals of *P. angustifasciatus* were commonly found resting on *R. peltatus* and because the geographic distribution of *P. angustifasciatus* largely overlaps that of *R. peltatus*, we suspect this plant may serve as host plant for this fly. From a biological perspective, the stem or root of this plant might be a suitable place for larvae or pupae to overwinter.

**Remarks.** The male of this species is mainly differentiated from the female by the broader width of the brown markings in cell r1 (thus the hyaline markings in cell r1 seem smaller in the male), and the crossband weaker posteriorly (Fig. 85). The conspecificity of the male and female of *P. angustifasciatus* was confirmed by observing mating behaviour in a cage in the summer of 2014 (Fig. 76).

**Pseudopelmatops continentalis** Zia & Chen, 1954
(Figs.87–88; 95, 104)


**Description** (supplement to the species description of Chen et al, 2010). Compound eye somewhat rough, with distinct projection; ommatidia not same size, which situating on projection bigger (Fig. 95). Occipital protuberance in male shaped as inverted trapezoid and somewhat bifid, distinctly delimited from occiput (Fig. 104); setae on posterior margin medium-sized and sparse.

**FIGURES 87–88 Pseudopelmatops continentalis** 87–88. Habitus (male) photos taken in Zhejiang, China (by Yong Wang)
**Distribution.** China (Henan, Hunan, Hubei, Zhejiang, Fujian, Sichuan, Yunnan, Guangxi, Guizhou and Shaanxi). Henan, Guangxi, Guizhou and Shaanxi are new province records for this species.


**Biology.** The Zhejiang collection site of this species was very similar to that of *P. angustifasciatus*. These two species were often observed in the same place and on the same day, and the behaviour of *P. continentalis* was also very similar to that of *P. angustifasciatus*.

Pseudopelmatops indiaensis Chen, 2010
(Figs. 96, 105)

Pseudopelmatops indiaensis Chen in Chen et al., 2010:3. Type-locality: Ranikhet, India. (H ♀ BPBM).

Description (supplement to the species description of Chen et al., 2010). Compound eye somewhat rough and rounded, without projection; ommatidia same size (Fig. 96). Occipital protuberance in male shaped like inverted trapezoid, and somewhat bifid with distinct border from occiput; setae on posterior margin medium-sized and sparse (Fig. 105).

Male. Similar to that of P. continentalis but with a very faint crossband over cell dm (D.L. Hancock, pers. comm.).

Distribution. India (Ranikhet).

Specimens examined. INDIA: Ranikhet, 22 June 1949, I. M. Newell, 1 HT ♀ (BPBM); Bhowali, nr Naini Tal, 5000ft, 20 September 1934, J.A. Graham, 1 ♂ (BMNH, checked by D.L. Hancock, pers. comm.).

**Pseudopelmatops nigricostalis** Shiraki, 1933


**Distribution.** China (Taiwan).

**Type data:** Syntypes 2♂ (depository reported as “Entomological Museum of the Government Research Institute, Taihoku, Formosa” but probably in National Institute of Agro-environmental Sciences, Kannondai, Japan), CHINA: Taiwan: Arisan, VII, X. (not examined).

**Pseudopelmatops yunnanensis** Chen, 2010


**Description** (supplement to the species description of Chen *et al.*, 2010). Compound eye not smooth in appearance, with small projection; ommatidia uniform in size (because the holotype is in poor condition, no photo of the compound eye has been taken; and because the occipital protuberance is invisible in present position, it is not described or photographed).

**Distribution.** China (Yunnan).

**Specimens examined.** CHINA: Yunnan, 195?. HT ♂ (IZCAS).

**Genus Soita Walker**


**New synonymy**

The genus *Soita* Walker was proposed by Walker (1865) for a single species, *S. psiloides* Walker, from Salawati, near New Guinea. Hardy (1974) added two species from the Philippines, *S. baltazarae* Hardy and *S. ensifer* Hardy, and provided a key to the three known species. Later, Hardy (1983) redescribed the female of *S. psiloides* and provided detailed figures of this species. Permkam and Hancock (1995) reviewed the diagnosis of this genus and recorded *S. psiloides* from Australia. Subsequently, the name *Phantasmiella* Hendel, 1914, was synonymized with *Soita* by Kagesawa (1998), who also provided a key to the four known species and studied the biology of *S. cylindrica* (Hendel) in detail. Norrbom and Hancock (2004) recorded this genus from New Caledonia.

*Soita* is characterized by the yellow slender body and wasp-like appearance, and head usually with 1 strong and strap-like orbital seta situated close to the middle of the frons, the abdomen usually having pairs of well-developed setae at least on the posterior margin of tergite 5. Head rounded in lateral view, with antenna longer than face and 1st flagellomere apically rounded (size and shape unknown in *S. ophioneum*); arista short plumose (unknown in *S. ophioneum*). Thorax yellow, lacking black marking, elongate, usually 2 times or more as long as wide. Scutum with complete transverse suture. Scutellum flat, shorter than wide, with 1–2 pairs of setae. Wing with veins R₁, R₄₊₅ and base of vein Cu with long, conspicuous setulae dorsally, R-M crossvein just beyond middle of cell dm; cell bcu with posterodistal lobe short and broad. Anatergite covered with long, fine setulae. Metathoracic postcoxal bridge broadly sclerotised. Mid tibia with 2 or 3 apical spurs, femora without rows of spines.

This genus generally resembles *Ichneumonomosoma*, but differs in having the base of vein Cu₅, setulose, 1 distinct and strap-like orbital seta, antenna longer than face, and most thoracic setae present (Permkam and Hancock, 1995). The host plants of *S. cylindrica* were recorded as Asclepiadaceae in Hokkaido and Honshu in Japan (Kagesawa, 1998). This is the only known biological information for this genus.

*Xaniosternum* was proposed as a monotypic genus by Enderlein (1920), who compared it with *Phantasmiella* Hendel, 1914, but not with *Soita*. Since then, no species have been added to *Xaniosternum*. However, *Phantasmiella* has been regarded as a synonym of *Soita* (Kagesawa 1998). According to Enderlein, *Xaniosternum* differs from...
Phantasmiella mainly as follows: head not elongated, rounded; scutellum with only 1 pair of setae; mesonotum on anterior half densely covered with short, stiff, upright setulae (not with only one longitudinal row of such setae on each side); abdomen very long, slender, strongly compressed laterally; first tergite in lateral view about 2.5 times as long as high posteriorly; crossvein R-M somewhat proximal to middle of cell dm. However, all these characters are shared with Soita. Except for the katepisternum having 3 rows of short brown spines extending longitudinally along the anteroventral margin, an autapomorphy of X. ophioneum, we have found no significant difference between Xaniosternum and Soita. Xaniosternum also agrees well with the description of Soita by Hardy (1974), and our morphology based cladistic analysis supports it as a natural member of Soita (Figs. 151–153). Therefore, we here consider Xaniosternum a subjective junior synonym of Soita.

Here we also describe one additional new species, S. infuscata Chen & Norrbom, from New Caledonia. Consequently, Soita now includes six species, with known distributions in the Oriental (Philippines, China), Australasian (Indonesia, Papua New Guinea, New Caledonia, Australia), Palaeartic (Japan) and Afrotropical (Equatorial Guinea) Regions.

**Key to known species of Soita Walker**

1. Scutellum with 2 pairs of setae (Figs. 120, 124); anepisternum and katepisternum anteroventrally with longitudinal row of short black spines along margin .......................................................... 2
   - Scutellum with 1 pair of setae (Figs. 131, 140, 145); anepisternum without short black spines along anteroventral margin . . . . 3
2. Scutum uniformly yellow to yellow-brown; wing with cell Sc brown, lacking slight infuscation at apices of vein Cu, and Dm-Cu (Fig. 123) (Luzon, Philippines) .......................................................... S. ensifera Hardy
   - Scutum yellow-brown with 2 pairs of narrow, pale yellow stripes; wing hyaline but slightly tinged with brown, cell Sc with apical half brown, and a distinct brown mark covering apex of vein Cu, and Dm-Cu (Fig. 119) (Indonesia, China and Japan) . . . . 3
3. Katepisternum anteroventrally with 3 marginal longitudinal rows of short brown spines; all body setae yellow to brown except for 1 pair strong orbital seta dark brown (Equatorial Guinea, Uganda). ........................... S. ophioneum (Enderlein) n. comb
   - Katepisternum lacking spines; body setae not as above .......................................................... 4
4. Head with 1 distinct long-oval black spot at base of orbital seta on each side and 1 irregular black spot on median occipital sclerite (Fig. 110); abdomen yellow to yellow-brown, but with black posterior bands on syntergite 1+2 and tergites 3–5 (Bohol, Philippines). .......................................................... S. baltazarae Hardy
   - Head without brown orbital and occipital marks; abdomen lacking black posterior bands on syntergite 1+2 and tergites 3–5 . . . 5
5. Wing with apices of radial cells infuscated (Fig. 128); abdominal tergites 3 and 4 with pair of outstanding submedial posterior setae; head yellow, with distinct narrow medial brown stripe on frons (New Caledonia) .......................................................... S. infuscata Chen & Norrbom, n. sp.
   - Wing with apices of radial cells not infuscated (Fig. 144); abdominal tergites 3 and 4 lacking pair of outstanding submedial posterior seta; head yellow to brown, without dark marks except ocellar tubercle or with vague medial brown stripe on frons (Indonesia, Papua New Guinea, Australia) .......................................................... S. psiloides Walker

**Soita baltazarae Hardy, 1974**

(Figs. 106–113)


**Diagnosis.** Head yellow, with paired distinct elongate oval black spot on base of orbital seta and 1 irregular black spot on median occipital sclerite (Figs. 109, 110). Scutellum with 1 pair of setae. Aneipisternum and katepisternum without short black spines extending longitudinally along anteroventral margin. Wing (Fig. 112) almost entirely hyaline except pterostigma brown and one very narrow, brownish diffuse band along anterior margins of cells r and r<sub>2+3</sub>. Abdomen (Fig. 111) yellow with distinct broad black bands on syntergite 1+2 and tergites 3–5 posteriorly.

**Distribution:** Philippines (Bohol).

**Specimen examined:** PHILIPPINES: Bohol: S Bullones, 366 m, 26 April 1955, C. R. Baltazar, HT ♀, (BPBM).

**Remarks.** This species appears to be most closely related to S. psiloides, but differs by having a diffuse narrow brownish band along the anterior margins of cells r<sub>1</sub> and r<sub>2+3</sub>, and by the abdomen having broad black bands on syntergite 1+2 and tergites 3–5 posteriorly.
**Soita cylindrica** (Hendel, 1914)
(Figs. 114–121)


**Soita** sp. Ito & Tamaki, 1995: 1787.

**Diagnosis.** Head almost entirely yellow, without dark marks except brown ocellar tubercle (Figs. 114–115, 117–118). Scutum (Fig. 120) yellow-brown with 2 pairs of narrow, pale yellow stripes, including submedial pair from anterior margin to level of dorsocentral seta, and postsutural sublateral pair from level of dorsocentral seta to posterior margin. Scutellum short, half as long as wide, with 2 pairs of setae, basal pair distinctly stronger than apical pair. Anepisternum and katepisternum each with row of short black setae along anteroventral margin. Wing (Fig. 119) hyaline but slightly tinged with brown, apical half of pterostigma brown, weak diffuse brown marks around the apices of veins R<sub>2+3</sub>, R<sub>4+5</sub> and M, and a more distinct brown mark covering most of crossvein DM-Cu and apex of vein Cu<sub>1</sub>.

**Distribution.** Japan (Hokkaido, Honshu), China (Taiwan), Indonesia (Sumatra).

**Specimen examined:** JAPAN: Hokkaido: Minamichitose chitose, 25 June 1997, N. Kagesawa, (Host: *Metaplexis japonica*, stem borer, Col. 8 June 1997) 1♂ (FFPRI).

**Host plants.** *Cynanchum caudatum* and *Metaplexis japonica* (Asclepiadaceae), recorded from Japan.

Remarks. This species is similar to *S. ensifera*, but differs by the yellow-brown scutum having 2 pairs of narrow, pale yellow stripes and the wing mostly hyaline but slightly tinged with brown, the pterostigma with apical half brown, and a distinct brown mark covering crossvein DM-Cu and the apex of vein Cu₁.

Biology. The biology of this species was described by Kagesawa (1998). The adults usually appear from mid July to early August in Japan. The mining by the larvae is initiated from the shoot tip of a host plant, and the larvae then feed and bore down the stem, sometimes making small side holes, but not forming a gall. The stem infested by *S. cylindrica* withers at its apex, and secretes white mucus from the side holes. In autumn or mid September, the fully grown larva turns upward and blocks the tunnel by forming a plug from plant tissues. It also prepares an elliptical or sometimes slitslike exit hole. The stem tends to break at the hole, allowing the adult to easily emerge from the stem in the next year. Pupariation takes place just below the plug, where the puparium overwinters. In the following summer, the adult emerges from the exit hole or broken stem. Both sexes were found to display “body swaying” and the characteristic wing movements observed in many other species of Tephritidae (Headrick & Goeden, 1994). The wing movement in *S. cylindrica* is, however, somewhat different from the “wing enation” described by Headrick & Goeden (1994), consisting of slight spreading and quick movement of the wings (Kagesawa, 1998).

*Soita ensifera* Hardy, 1974
(Figs.122–126)

*Soita ensifera* Hardy, 1974: 152. Type-locality: Philippines. Luzon, Laguna: Mount Makiling (HT ♂ MCSNM)

**Diagnosis.** Head entirely yellow, lacking any dark spots on occiput, front or face (Figs. 125–126, the irregular black area on the frons is a reflection of the inside of the head). Thorax entirely yellow to yellow-brown (Fig. 124), scutellum with 2 pairs of setae, anepisternum and katepisternum with row of short black spines extending longitudinally along anteroventral margin. Mid tibia with 3 strong apical spurs. Abdomen entirely yellow to yellow-brown, male with tergite 5 having 8 strong setae at apex.

**Distribution:** Philippines (Luzon).

**Specimen examined:** PHILIPPINES: Luzon, Samar, Baker, 1♂ (USNM).

**Remarks.** This species resembles *S. psiloides* by the almost entirely hyaline wing and the entirely yellow thorax, abdomen and legs, but differs in having 2 pairs of scutellar setae, the wing lacking slight infuscation on crossvein DM-Cu and apex of vein Cu₁, the katepisternum very narrow, over 2 times longer than wide and with a longitudinal row of short black setae ventrally extending onto the anepisternum (Hardy, 1974).

**Soita infuscata** Chen & Norrbom, new species.
(Figs.127–134)

*Soita* sp. Norrbom & Hancock, 2004: 76.

**Diagnosis.** Head yellow, with distinct narrow medial brown stripe on frons. Scutum mostly pale brown, but with broad medial postsutural yellowish area. Anepisternum and katepisternum without short black spines along anteroventral margin. Wing yellow, with pterostigma dark brown, apices of radial cells and mark on crossvein DM-Cu pale brown. Abdomen with syntergite 1+2 and tergite 3 yellow and tergites 4 and 5 dark brown; tergites 3 and 4 each with pair of outstanding submedial posterior setae.

**Description.** Male: body length 8.8 mm, wing length 6.0 mm.

Head (Figs. 132–133): Yellow except frons with distinct narrow medial brown stripe and ocellar tubercle dark brown to black; antenna and labella yellow-brown to brown. Head almost as long as high, with eye nearly round, frons gently sloping, antenna situated at middle of head, and face short. Occiput moderately swollen. Frons not parallel-sided, margins slightly convergent anteriorly. Antenna distinctly longer than face, with 1st flagellomere rounded dorsoapically, about 3 times as long as wide; arista plumose, longest ray about 1/3 width of 1st flagellomere. One pair of strong orbital setae (orbital seta itself lost, but socket distinctly larger than frontal seta socket) and 2 pairs frontal setae; orbital seta at about anterior 2/5 of frons, frontal setae close to each other and near anterior margin of frons, aligned just posterior to posterior margin of lunule. Vertical setae present (medial vertical setae lost, but sockets obvious), ocellar seta small and hairlike, genal seta absent.

Thorax (Figs. 130–131). Entirely yellow to brown. Transverse suture complete (middle part hidden by pin). Metathoracic, postcoxal bridge heavily sclerotized. Scutum mostly brown, but broadly yellowish medially posterior to transverse suture; almost parallel-sided, about 3 times as long as wide. Scutellum yellow, very short, less than half as long as wide, of pair of setae. Anepisternum and katepisternum without short black spines along anteroventral margin. Other thoracic setae: 1 postpronotal, 2 notopleural, 1 postsutural supra-alar, 1 postalar, 1 intra-alar and 1 dorsocentral setae present and black.

Wing (Fig. 128). Mostly pale yellowish. Pterostigma dark brown and about half as long as cell c. One broad diffuse brown mark covering apical sixth of wing including apices of veins R₂₃, R₄₅ and M, another diffuse brown mark covering apex of vein Cu₁ and most of crossvein DM-Cu. Vein R₂₃ densely setulose dorsally from base to apex. Vein Cu₁ setulose dorsally from base to slightly proximal to crossvein R-M. Legs. Fore leg yellow to yellow-brown (mid and hind legs lost).

Abdomen (Fig. 134). Syntergite 1+2 and tergite 3 yellow, tergites 4–5 dark brown. Tergites 3 and 4 each with pair of outstanding submedial posterior setae, tergite 5 with large posterior setae missing (but large sockets present). Tergites 3 and 4 about same length, tergite 5 slightly longer than tergite 4.

Female: Unknown.

**Distribution.** New Caledonia.

**Type data:** Holotype ♀ (INHS), NEW CALEDONIA: Prov. Sud, 9.3 km NW Sarraméa, 21°35′04″S, 165°47′18″E, 445 m, Malaise trap along forest path, 23 January 1996, M.E. Irwin, D.W. Webb & E.I. Schlinger.

**Etymology.** The name of this species is an adjective referring to the infuscated apical area of the wing.

**Remarks.** This species is generally similar to *S. psiloides*, differing from it by the yellow wing, with the apices
of the radial cells infuscated; abdomen with tergites 3 and 4 having a pair of outstanding submedial posterior setae, and head yellow, with a distinct narrow medial brown stripe on the frons.

**Soita ophioneum** (Enderlein), 1920, new combination

*(Figs. 135–142)*


**Diagnosis.** Head entirely yellow except brown ocellar tubercle, lacking dark spots on occiput, frons and face. Thorax entirely yellow to yellow-brown, scutellum with 1 pair of setae, katepisternum with 3 rows of short brown spines extending longitudinally along anteroventral margin. Wing uniformly yellow, without dark markings. All body seta yellow to brown except for 1 pair of strong orbital seta dark brown. Abdomen yellow-brown with some vague dark brown markings.


**Description.** *Male:* body length 13.0 mm, wing length 9.8 mm.

Head (Figs. 135–136): entirely yellow except ocellar tubercle brown, lacking dark spots on occiput, frons and face. Head wider than high, frons sloping, antenna situated at middle of head. Occiput distinctly swollen. Frons parallel-sided, margins not convergent anteriorly. One pair of strong dark brown orbital setae and 2 pairs weak and yellow-brown frontal setae; orbital seta at about anterior \(\frac{3}{4}\) of frons, frontal setae close to each other and near anterior margin of frons, aligned just to posterior margin of lunule. Vertical setae present (setae themselves lost, but sockets obvious), ocellar seta absent, genal seta present.
Thorax (Figs. 135,140). Entirely yellow to yellow-brown. Transverse suture complete. Metathoracic, postcoxal bridge heavily sclerotized. Scutum almost parallel-sided, about 3 times as long as wide. Scutellum very short, less than half as long as wide, with 1 pair of setae. Katepisternum with 3 rows of short brown spines extending longitudinally along anteroventral margin. Thoracic chaetotaxy: 2 pairs scapular, 1 dorsocentral, 1 scutellar, 1 postpronotal, 2 notopleural, 1 poststural supra-alar, 1 postalar, 1 intra-alar, 2 anepisternal, 1 anepimeral, 1 katepisternal setae present and dark brown; prescutellar acrostichal seta present.

Wing (Figs. 141–142). Uniformly yellow, without dark markings. Pterostigma yellow-brown and about half as long as cell c. Vein R_{4+5} densely setulose dorsally almost from base to apex. Vein Cu_{1} setulose dorsally from base to slightly proximal to crossvein R-M. Legs. Uniformly yellow, mid tibia with 2 large black apicoventral spurs (one is broken).

Abdomen (Fig. 138). Yellow-brown with some vague dark brown markings. Syntergite 1+2 with pair of outstanding submedial posterior setae, tergite 5 with large posterior setae (several missing, but large sockets present). Tergites 3 and 5 about same length, tergite 4 slightly longer than tergite 3 and 5.

Female: Unknown.

Distribution: Equatorial Guinea.

Specimen examined: EQUATORIAL GUINEA: Nkolentangan, November 1907 to May 1908, S.G. Tessmann, ♂ Holotype (ZMHB).

Remarks. This species resembles S. ensifera and S. cylindrica in having the katepisternum with short spines extending longitudinally along the anteroventral margin, but it differs from them by having only 1 pair of scutellar setae, anepisternum without short spines, and wing uniformly yellow.

Soita psiloides Walker, 1865
(Figs.143–150)


Diagnosis. Head (Figs. 148–149) entirely yellow to brown, usually lacking dark spots on occiput, frons or face, but 3 of Papua New Guinea specimens with a vague medial dark mark on frons; 1 pair of strong and strap like orbital setae and 2–3 pairs of small frontal setae. Thorax (Fig. 145) entirely yellow to yellow-brown; postpronotal, postalar, dorsocentral, anterior supra-alar, and presutural setae dark brown to black; notopleural, anepisternal, anepimeral and katepisternal setae yellow to yellow-brown. Mid tibia with 3 ventral setae at apex, 2 moderately long, 1 short. Scutellum with 1 pair of setae. Anepisternum and katepisternum without row of short black spines. Wing (Fig. 144) almost hyaline except pterostigma brownish yellow apically and slight infuscation bordering apices of veins R_{2+3}, R_{4+5} and Cu_{1}. Abdomen (Fig. 147) entirely fulvous. Female with oviscus short, scarcely longer than wide. Aculens short and thick, with 4 sharp toothlike points at apex, and minute serrations on apical margins (Fig. 150). Three elongate spermathecae. Male genitalia with surstyli short and thick, covered with fine, pale hairs (Fig. 146).

Distribution: Indonesia, Papua New Guinea, Australia (northeast Queensland).

FIGURES 143–150 *Soita psiloides* 143. Habitus (male), lateral view; 144. Wing; 145. Head and scutum, dorsal view; 146. Epandrium and surstyli, lateral view; 147. Abdomen, dorsal view; 148. Head, lateral view; 149. Head, frontal view; 150. Aculeus, dorsal view.
Phylogenetic Relationships

Phylogenetic analysis based on morphology

To investigate phylogenetic relationships among the four genera and their species, especially the stalk-eyed fruit flies, *Pelmatops* and *Pseudopelmatops*, all 19 species of these four genera were included in the cladistic analysis as ingroup members (Table S1). Twenty-seven characters were defined from morphological study of the ingroup and outgroup species, which are listed below.

List of characters

**Head**
- 0. Ocellar seta: (0) present; (1) absent
- 1. Postocellar seta: (0) present; (1) absent
- 2. Lateral vertical setae: (0) present; (1) absent
- 3. Postocular setae: (0) present; (1) absent
- 4. Orbital setae: (0) 2 pairs; (1) 1 pair, shape and position normal; (2) 1 pair, strong and situated at middle of frons; (3) absent
  (the character state transformation series set as $o \rightarrow i \rightarrow s$)
- 5. Frontal setae: (0) 3 pairs; (1) 2 pairs; (2) 1 pair; (3) absent
- 6. Genal seta: (0) present; (1) absent
- 7. 1st flagellomere width to length ratio: (0) 0.45–0.65; (1) 0.20–0.40
- 8. Length of 1st flagellomere to length of face ratio: (0) 0.3–0.7; (1) 0.8–1.2
- 9. Length of eye stalk: (0) eye stalk absent; (1) eye stalk/scutum length ratio 1.0–2.0 in male; (2) eye stalk/scutum length ratio 2.5–3.3 in male; (3) eye stalk/scutum length ratio 3.5–4.5 in male
- 10. Bands on eye stalk or lateral part of frons or parafacial (homologous to eye stalks): (0) without markings; (1) with only frontal band, or with dorsal band obscure and short if present; (2) with long and distinct frontal and dorsal bands
- 11. Head shape in lateral view: (0) higher than long; (1) as high as long or longer than high

**Thorax**
- 12. Postpronotal seta: (0) present; (1) absent
- 13. Prescutellar acrostichal seta: (0) present; (1) absent
- 14. Dorsocentral seta: (0) present; (1) absent
- 15. Scutellar setae: (0) 2 pairs; (1) 1 pair
- 16. Number of strong apical spurs on mid tibia: (0) 1; (1) 2; (2) 3
- 17. Vein R$_{xy}$: (0) wholly setulose; (1) setulose from the base to R-M or DM-Cu; (2) bare or with only 1–2 setulae basally
- 18. Cell bcu posterodistal lobe: (0) acute, forming angle distinctly less than 45º; (1) short and broad, forming angle equal to or greater than 45º
- 19. Scutum width/length ratio: (0) 0.70–0.90; (1) 0.60–0.69; (2) 0.40–0.59
- 20. Transverse suture on scutum: (0) clearly incomplete; (1) complete or nearly so
- 21. Metathoracic postcoxal bridge: (0) semimembranous medially or membranous; (1) broadly sclerotised

**Abdomen**
- 22. Abdomen shape: (0) narrowed anteriorly and expanded posteriorly; (1) parallel-sided or nearly so
- 23. Abdominal syntergite 1+2 and tergite 3 width to length ratio: (0) 1.0–1.3; (1) 0.5–0.8; (2) 0.1–0.4
- 24. Aculeus width to length ratio: (0) 0.10–0.20; (1) 0.25–0.35; (2) 0.40–0.50
- 25. Female aculeus tip: (0) not serrate or dentate; (1) apicolaterally serrate or dentate; (2) dorsally serrate (the character state transformation series set as $1 \rightarrow 0 \rightarrow 2$)
- 26. Female aculeus tip: (0) with setae; (1) without setae

Most of the ingroup species are large and their abdomens are usually bent downwards, so we utilized the length and width of tergites 1+2+3 for character 24 instead of the whole abdomen; the width was measured at the middle of the first three tergites. For *I. consors*, the states of characters 25 and 26 were scored based on the description of Permkm and Hancock (1995). For *Pelmatops fukienensis*, the state of character 9 was scored based on the figure of Zia & Chen (1954) because the head of the examined male is missing. In *Soita ensifera*, the state of character 16 was scored based on the description of Hardy (1974) because some spurs on the mid tibia were missing on the examined specimen. In *S. cylindrica*, the states of characters 24, 25 and 26, which pertain to the female, were scored based on the figures of Kagesawa (1998) because only one male specimen was examined. The complete data matrix is shown in Table S2. In the TNT analyses, characters were treated as additive and Characters 4 and 25 were scored by the 'step-matrix' option in the 'character settings' based on the character state transformation series shown at the end of those characters in the list.

The morphological matrix was analyzed using TNT (Goloboff et al. 2008). It was searched by the “implicit enumeration” option with “auto-collapse searches” off. The analysis resulted in 5 most parsimonious trees of 79
steps. None of the trees differ at the genus level. The consensus tree (Fig. 151, with the common synapomorphies mapped) was calculated by “strict (=Nelson)” using all trees and all taxa. We resampled the matrix with the standard bootstrap method using 100 replicates, with the resulting consensus tree shown in Fig. 152. As in the first consensus tree, the monophyly of *Ichneumonosoma, Pelmatops, Pseudopelmatops* and *Soita* is well supported, and the stalk-eyed fruit flies are hypothesized to be more closely related to *Ichneumonosoma* than to *Soita*. Among other Adramini species included, *Adama apicalis* appears more closely related to these 4 genera than the others. The interspecific phylogenetic relationships of *Ichneumonosoma* and *Soita* were partly resolved, and that of *Pelmatops* was well resolved. However, that of *Pseudopelmatops* remained unresolved.

**FIGURE 151.** Consensus tree of *Ichneumonosoma, Pelmatops, Pseudopelmatops, Soita* and outgroup members obtained by TNT (implicit enumeration) based on 27 adult morphological characters, with the common synapomorphies mapped on the cladogram.

**FIGURE 152.** Consensus tree of *Ichneumonosoma, Pelmatops, Pseudopelmatops, Soita* and outgroup members obtained by TNT (resample the matrix with standard bootstrap method by using replicates 100 and traditional search) based on 27 adult morphological characters, with bootstrap shown next to the branches.
The phylogenetic tree resulting from Bayesian analysis (Fig. 153) differed slightly from the TNT consensus trees. In both the Bayesian and TNT trees, *Ichneumonosoma*, *Pelmatops*, *Pseudopelmatops* and *Soita* were each monophyletic, and the clade of stalk-eyed fruit flies (*Pelmatops + Pseudopelmatops*) was well supported. The sister relationships between *I. consors* and *I. heinrichi*, *Pe. ichneumoneus* and *Pe. tangliangi*, and *S. cylindrica* and *S. ensifera*, are recognized in all of the trees. On the other hand, the Bayesian tree differs from the TNT trees in that *Adrama apicalis*, *Ichneumonosoma*, *Soita*, and the stalk-eyed flies form an unresolved polytomy. *Ichneumonosoma* is not hypothesized to be closer to the stalk-eyed fruit flies than *Soita*.

**FIGURE 153.** Bayesian tree of *Ichneumonosoma*, *Pelmatops*, *Pseudopelmatops*, *Soita* and outgroup members obtained by MrBayes (10000 generations sampling trees every 10 generations, using four chains and GTR+Gamma model.) based on 27 adult morphological characters, with posterior probabilities shown next to the branches.

**FIGURE 154.** MP tree (A) and Bayesian tree (B) of *Ichneumonosoma*, *Pelmatops*, *Pseudopelmatops*, *Soita*, outgroup members and one Diptera larva inferred from 28S sequences of 23 taxa. Values indicate clade bootstrap support.
Phylogenetic analysis based on 28S and COI genes

Due to lack of sufficient fresh material, the following analysis of relationships inferred from molecular data is far from complete. However, at this stage, it might provide meaningful supplemental information to the morphology-based classification.

The final alignment of the 28S sequences for 23 taxa was 403 bp. Both the MP (Fig. 154A) and Bayesian tree (Fig. 154B) resulting from the analyses are similar and agree to some extent with the trees from the morphological analyses (Figs. 151–153). The monophyly of Pseudopelmatops is strongly supported by the molecular analyses (Fig. 154); however, relationships among the species and geographic populations are not well defined. Unlike the morphological trees, the single species of Ichneumonosoma is not grouped in the same clade as Pseudopelmatops, Pelmatops and Soita in either tree; it is grouped in a clade with Cyclopsia species. A clade including Pseudopelmatops, Pelmatops and Soita is supported in both trees. The hypothesis supported by the morphological analysis that the stalk-eyed fruit flies (Pelmatops + Pseudopelmatops) are more closely related to each other than to Soita and Ichneumonosoma (Fig. 151–153) was not supported by either the MP and Bayesian analyses, although two clades, Pseudopelmatops and Pelmatops + Soita are supported in both the MP and Bayesian trees (Fig. 154).

The final alignment of the COI dataset for 16 taxa was 585 bp. The MP tree (Fig. 155A) and Bayesian tree (Fig. 155B) differed slightly, with the Bayesian tree proving more similar to the morphological trees (Figs. 151–153). In the MP tree, Pelmatops is grouped with Euphranta, whereas in the Bayesian tree Pelmatops and Pseudopelmatops form a monophyletic clade. In both COI trees, Pelmatops and Pseudopelmatops are each strongly supported as monophyletic, although their interspecific and geographic population relationships are unresolved. In the Pelmatops clade, one sample of P. ichneumoneus is grouped with the single specimen of P. tangliangi rather than the other specimen of P. ichneumoneus. In the Pseudopelmatops clade, neither species is supported as a monophyletic group.

Phylogenetic relationships based on the combined dataset of morphology characters, 28S and COI genes

The combined dataset contained 32 taxa and 1015 characters. The morphological data comprised 27 characters, the aligned 28S dataset comprised 403 characters, and the COI dataset comprised 585 characters. Bayesian analysis resulted in a phylogenetic tree (Fig. 156) which was different from the morphological and molecular trees.

In the Bayesian phylogeny, each of the four genera, Ichneumonosoma, Pelmatops, Pseudopelmatops and Soita, were supported as monophyletic groups (PP=97, 99, 100, 82, respectively), and Soita was strongly supported as the sister group of the clade of stalk-eyed fruit flies (PP=100). However, Ichneumonosoma was nested in another clade with Cyclopsia and Euphranta. The sister relationships between Pelmatops ichneumoneus and P. tangliangi, and between S. cylindrica and S. ensifera, were well and moderately supported respectively (PP =96, 87). However, the
sister relationship between *I. consors* and *I. heinrichi*, was poorly supported (PP=56). Among the other Adramini species included, *Adrama apicalis* was situated basally, differing from the morphological trees (Fig. 151–153). However, the interspecific phylogeny in the four genera was consistent with both the morphological and molecular trees. In *Ichneumonosoma* and *Soita*, the species relationships are partially resolved; in *Pelmatops* they are fully resolved, but in *Pseudopelmatops* they are unresolved.

**FIGURE 156.** Bayesian tree of *Ichneumonosoma*, *Pelmatops*, *Pseudopelmatops*, *Soita* and outgroup based on the combined dataset of morphological characters and 28S rDNA (28S) and the mitochondrial cytochrome c oxidase I (COI) sequences (1000000 generations sampling trees every 1000 generations, using four chains, GTR+Gamma model for morphology characters, GTR+Invgamma model for molecular characters), with posterior probabilities shown next to the branches and head anterior view of representative species in each genus mapped on the tree.

**FIGURES 157–159.** Stem mine of larva of Sesiidae on *Rubus peltatus*. Fig. 157 ‘Blocking cap’ outside opening in stem; Fig. 158 Mine opening with ‘blocking cap’ removed; 159. Larva of Sesiidae in mine (by Yong Wang and Xiao-lin Chen)
Phylogenetic implications for the evolution of the stalk-eyed fruit flies

The stalk-eyed fruit flies, comprising *Pelmatops* and *Pseudopelmatops*, are easily distinguished from other tephritids by their unusual head structure, with the eyes borne at the ends of stalks. They were recognized as a subtribe of Adramini, namely Pelmatopina, by Wang (1996). This group is mainly restricted to the Oriental tropics and subtropics, and most of the species are known to occur in southern China. However, *Pe. ichneumoneus* extends westwards to Nepal and India and south to Thailand, *Ps. angustifasciatus* occurs in Vietnam, *Pe. tangliangi* also occurs in Vietnam and India, and *Ps. indiaensis* is so far known only from India (Chen et al., 2010). On the other hand, both *Soita* and *Ichneumonosoma* are more widely distributed than the stalk-eyed fruit flies, the range of *Soita* extends across the Oriental (Philippines, China), Australasian (Indonesia, Papua New Guinea, New Caledonia, Australia), Palaearctic (Japan) and Afrotropical (Equatorial Guinea) Regions, whereas that of *Ichneumonosoma* includes the Oriental (Thailand, Malaysia, India) and Australasian (Indonesia, Papua New Guinea, Australia) Regions (Walker, 1865; Enderlein, 1920; Hardy, 1974, 1983; Permkan and Hancock, 1995; Kagesawa, 1998; Norrbom and Hancock, 2004).

*FIGURES 160-163* Adults of *Pseudopelmatops angustifasciatus* on mined stems of *Rubus pellatus*. Fig. 160. Male of *P. angustifasciatus* on ‘blocking cap’ on 29 August 2014; Fig. 161. The same male on the stem above the ‘blocking cap’ on early morning of 30 August 2014; Figs. 162-163. Interacting male and female of *P. angustifasciatus* above the ‘blocking cap’ on 29 August 2014 (by Yong Wang and Xiao-lin Chen).
The origin and reason for the evolution of the stalk-eyed fruit flies is a long-standing enigma that was difficult to address without knowledge of their phylogenetic relationships. Results of our analyses of 28S (Fig. 154) and the combined data (Fig. 156) suggest that Soita is the sister group of the stalk-eyed fruit flies, whereas the morphological analysis (Figs. 151–153) places Ichneumonosoma as their sister group. The unresolved interspecific relationships of Pseudopelmatops might imply a rapid radiation process in this genus. The well resolved interspecific relationships in Pelmatops suggest that further study of P. fukienensis, the basal species, is crucial to understand the origin of Pelmatops and its separation from Pseudopelmatops. Pelmatops tangliangi has the longest eye stalk in the two genera (clearly longer than the body in the male), and it is differentiated from the closely related species, P. ichneumoneus, mainly by this character and the shape of the eye (Figs 91–92). In the analysis based on COI (Fig. 155), one sample of P. ichneumoneus is grouped with the single specimen of P. tangliangi rather than the other specimen of P. ichneumoneus, which might indicate that the speciation of P. tangliangi is very recent.
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Author Contributions

Xiao-lin Chen, Allen Norrbom, and Chao-dong Zhu conceived and designed the project and molecular experiments. Xiao-lin Chen, Allen Norrbom, and Amnon Freidberg performed the taxonomy and morphological identification, description and analysis. Xiao-lin Chen, Sajedul Islam, Douglas Chesters and Chao-dong Zhu performed the molecular experiments and data analysis. All of the authors write and revise the manuscript.

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