

A new species of *Soritia* WALKER, 1854 from Taiwan, with phylogenetic comments on the genus (Lepidoptera, Zygaenidae, Chalcosiinae)

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Abstract: A new chalcosiine zygaenid species, *Soritia azurea* sp. n., is described from the Shuan-Guei-Hu Wildlife Reserve Area in southern Taiwan; male holotype in NMNS, Taichung, Taiwan. Its metallic blue hindwing in the male is unique amongst all *Soritia* species. Morphology of copulatory structures and colour pattern suggest that *S. azurea* may form a monophyletic group with *S. choui* YEN & YANG, 1998 (Taiwan), *S. elizabetha* (WALKER, 1854) (China) and an undescribed species from northern Vietnam (= *Eterusia proprimarginata* sensu ENDO & KISHIDA, 1999, nec PROUT, 1918). The true *Soritia proprimarginata* (PROUT, 1918) is not related to this group but is closer to the species-complex of *Soritia pulchella* (KOLLAR, 1844).

Keywords: Sexual dimorphism, pregenital abdominal segment, male genitalia, incompatible characters.

Eine neue *Soritia* WALKER, 1854 von Taiwan, mit phylogenetischen Anmerkungen zur Gattung (Lepidoptera, Zygaenidae, Chalcosiinae)

Zusammenfassung: Eine neue Art der Zygaenidae: Chalcosiinae, *Soritia azurea* sp. n., wird aus dem Naturschutzreservat Shuan-Guei-Hu in Südtaiwan beschrieben; männlicher Holotypus in NMNS, Taichung, Taiwan. Mit den metallisch blauen Hinterflügeln des Männchens ist die Art einmalig in der Gattung. Nach der männlichen Genitalmorphologie und der Flügelzeichnung gehört die neue Art vermutlich in eine monophyletische Gruppe zusammen mit *S. choui* YEN & YANG, 1998 (Taiwan), *S. elizabetha* (WALKER, 1854) (China) und einer unbeschriebenen Art aus dem nördlichen Vietnam (= *Eterusia proprimarginata* sensu ENDO & KISHIDA, 1999, nec PROUT, 1918). Die echte *Soritia proprimarginata* (PROUT, 1918) ist nicht nah verwandt mit dieser Gruppe, sondern gehört zu dem Artenkomplex von *Soritia pulchella* (KOLLAR, 1844).

Introduction

The Taiwanese species of the genus *Soritia* WALKER, 1854 (type-species: *Chalcosia leptalina* KOLLAR, [1844] 1848, = *Chalcosia pulchella* KOLLAR, [1844] 1848) have recently been revised (YEN & YANG 1998), and two species (*Soritia pulchella strandi* KISHIDA, 1995, and *Soritia choui* YEN & YANG, 1998) were verified as being, then, the only Taiwanese representatives of *Soritia*. In 1996, during a coleopterological survey in the Shuan-Guei-Hu Nature Reserve Area in S. Taiwan, another new species with a very distinct wing pattern was discovered. The new species represents a previously unknown lineage within *Soritia* and seems to be closely related to "*Eterusia proprimarginata*" sensu ENDO & KISHIDA (1999). In the present study, the new species is described, and a discussion of its relationships within the genus is provided.

Morphological dissection techniques followed the general protocol described by HOLLOWAY et al. (1987); terminology

used in the present study mostly follows KLOTS (1970) and SCOBLE (1992) with slight modification. The type material of the new species will be deposited in National Museum of Natural Science, Taichung, Taiwan (NMNS).

The sources of specimens examined for relevant species are The Natural History Museum, London (BMNH), Deutsches Entomologisches Institut, Eberswalde (DEI), Hokkaido University, Faculty of Agriculture, Sapporo (HUFU), Museum National d'Histoire Naturelle, Paris (MNHN), National Museum of Natural Science, Taichung (NMNS), National Taiwan University, Taipei (NSMT), Taiwan Forestry Research Institute, Taipei (TFRI), Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK), and Zoologisches Museum für Naturkunde, Humboldt University, Berlin (ZMHB).

Taxonomic accounts

***Soritia azurea* sp. n.** (Figs. 1A–D, 2A–D, 3A–F, 4)

Holotype: ♂, Taiwan: Pingtung Hisen (= County), Wutai, Shuan-Guei-Hu [literally Two-Ghost-Lakes] Nature Preserve Area, 2300 m, 21. viii. 1996, W. I. CHOU leg. [NMNS].

Paratype: 1 ♀, same data as holotype [NMNS].

Etymology: The specific name "azurea" refers to the bright metallic blue hindwing in the ♂.

Diagnosis

Length of forewing: ♂ 21 mm, ♀ 24 mm. A medium-sized chalcosiine moth with significant sexual dimorphism. ♂ forewing black with yellow patches, hindwing metallic blue. ♀ forewing yellow with several spots near discoidal cell. ♂ easily distinguishable from ♂♂ of *Eucormopsis lampra* JORDAN, 1907 and the *Cyclosia papilionaris* (DRURY, 1773) and *C. macularia* (GUÉRIN-MÉNÉVILLE, 1843) species complexes by having yellow patches on forewing. ♀ distinct from that of *S. elizabetha* (WALKER, 1854) (Figs. 1K–L, 4C) in weaker hindwing spots, shorter forewing length, narrower lamella antevaginalis and lacking appendix burase.

♂ (Figs. 1A–B). Head: Vertex slightly crested medially, covered by metallic dark blue scales; frontoclypeus protruded anteriorly, covered by creamy white scales; labial palpus 3-segmented, as long as diameter of compound eye; maxillary palpus minute; antennal length 7.1 mm, bipectinate; flagellar segments 52, black, 0.6–0.8 mm; chaetosemata developed, with black scales associated with sensillae trichodea; proboscis developed. Thorax: Prothorax with patagia and parapatagia black, tinged with dark blue; tegula bright yellow; mesothorax and metathorax blackish blue dorsoventrally; all legs black with grayish white scales ventrally. Forewing: Upperside

ground colour black, submarginal zone with 6 yellow patches on r_{4+5} , m_1 , m_2 , cua_1 and cua_2 cells, respectively; discoidal cell with a large orbicular yellow patch at distal edge and a long yellow stripe from base to $\frac{1}{2}$ of forewing length; an elongate yellow patch, plus a spherical yellow spot, parallel to lower margin of discoidal cell; pattern of underside as upperside, but with bright metallic sheen from base to $\frac{1}{2}$ of forewing. Hindwing: Upperside metallic blue with black border at upper margin and costal margin; underside background colour black, pattern similar to that of forewing but with 2 lunule patches on m_2 and m_3 cells and another 2 rows of rounded spots on cua_1 and cua_2 cells, respectively. Abdomen: Tergum black, sternum white, a row of lateral black dots present on each segment. Scent organ described by TARMANN (1992a) not developed in this species, androconial bristles arising from hindwing base absent, abdominal lateral pouch weakly present before spiracle.

♀ (Figs. 1C–D). Head: Vertex and frontoclypeus as in ♂, covered by creamy yellow scales; antennal length 7.4 mm, bipectinate with short and serrate rami; chaetosemata developed, with yellow scales associated with sensillae trichodea; proboscis developed; other cranial appendages as in ♂. Thorax: Prothorax with patagia, parapatagia and tegula yellow; mesothorax and metathorax yellow dorsoventrally; all legs black with light yellow scales ventrally. Forewing: Upperside bright yellow, apex black, 3 black spots on m_2 , m_3 and cua_1 cells, respectively, discoidal patch at $\frac{5}{6}$ of cell and divided by medial vein; underside similar to upperside but with lighter ground colour. Hindwing: Light yellow on upperside, spots on m_2 – cua_1 cells not as clear as those on underside; discoidal patch on underside at about $\frac{5}{6}$ of cell and separated into two small spots. Abdomen: Tergum light yellow dorsoventrally with metallic blue annular ring at anterior margin of each segment. Abdominal scent organ more developed than that in male but not strongly sclerotized.

♂ genitalia and pregenital abdominal segment (Figs. 2A–D, 3A–F). Uncus and tegumen fused, not articulated; uncus somewhat rectangular laterally and dorsally with apex and base narrower, apex rounded with scattered sensory setae; subsclerite absent; tegumen narrow laterally, curved outwards at $\frac{1}{2}$, bases of both sides of tegumen connected medially by an anteriorly extended plate-like sclerite, a pair of arm-like apodemes which serve as attachment for m_4 muscles arising from base of tegumen and running down to base of vinculum; a pair of peculiar sclerotized structure with unknown function present laterally at articulation between tegumen and vinculum. Vinculum slender laterally, with saccus extended anterodorsally. Valva strongly sclerotized, bases of each side fused, immovable, cucullus membranous with some lateral setae, saccus broader at base, swollen medially and followed by a digital process at top, surface of saccus setose and slightly ridged. Juxta and anellus absent. Phallus without prominent phallobase; a ventral digital process present medially; aedeagus sharp, bending

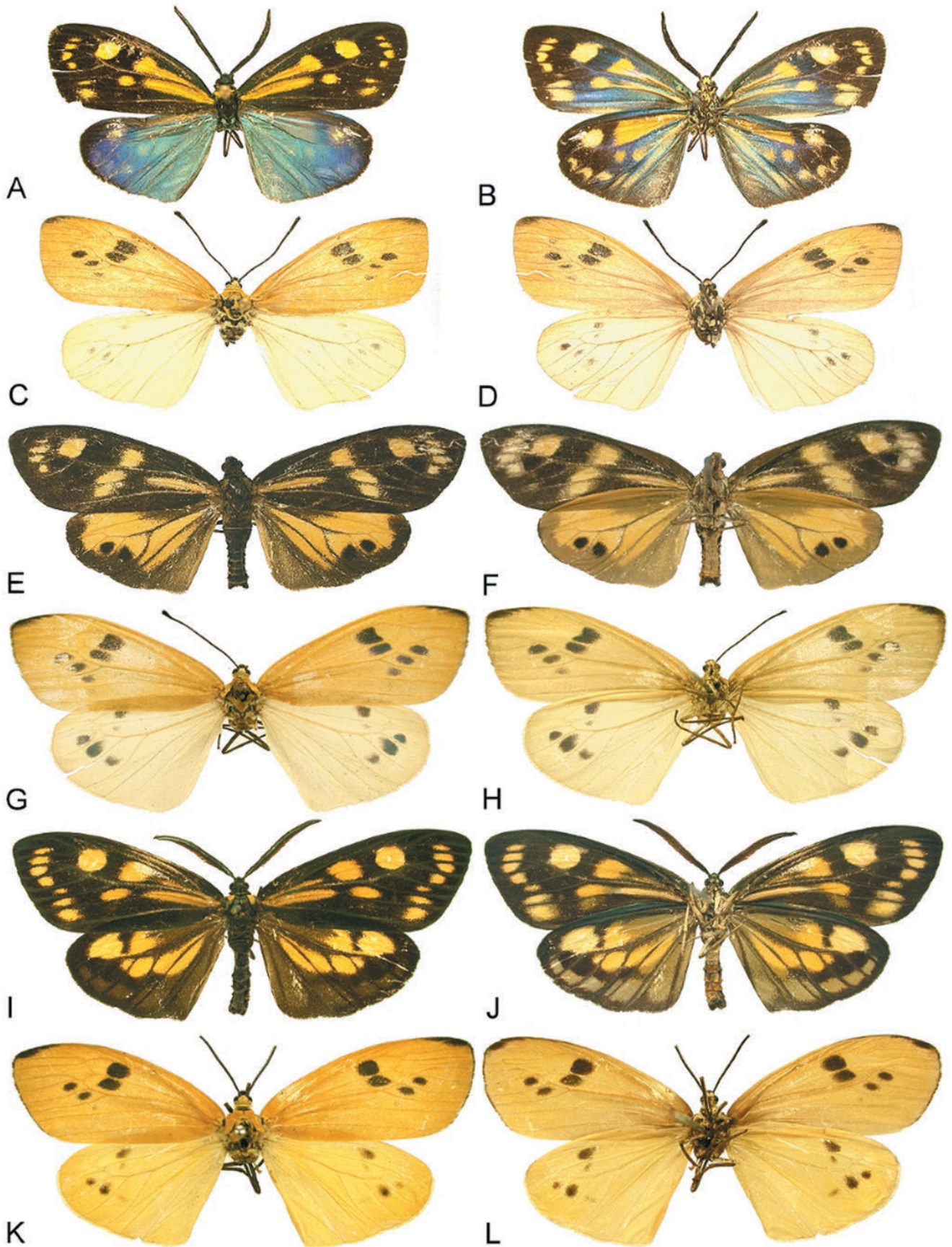
downwards and surrounded by wrinkled diaphragma which is weakly sclerotized; bulbus ejaculatorius cap-like, swollen medially and finger-like near end; vesica and cornutus not present. Pregenital (eighth) abdominal segment differentiated into uncus-like and valva-like structures; tergite trapezoidal dorsally with caudal margin emarginated to $\frac{1}{3}$ of length; a bifurcate structure with base derived from ventral part of caudal margin and broadened cephalolaterally, two slender arms with curved apical portion running straight down near medial base of sternite; sternite somewhat rectangular ventrally and laterally with a pair of elongate processes extended posterodorsally; posterior process with dense thick setae on inner surface of lateral part and shorter setae on lower and medial parts; ventromedial part of sternite concave ventrally.

♀ genitalia (Fig. 4A–B). Eighth tergite with anterior margin deeply incised; when fully extended, apophyses anteriores reaching to approximately $\frac{1}{4}$ of 7th abdominal segment; apophyses posteriores slender, extending before anterior margin of 7th tergite; a slender forked apodeme arising from middle. Bursa copulatrix with corpus bursae oblique, slightly grained, reaching to anterior margin of 6th segment; appendix bursae and signa absent; ductus bursae slender; ostium surrounded by a heavily sclerotized lamella antevaginalis. Ductus seminalis arising near corpus bursae. Pseudobursa present. Ductus spiralis and lagena present; receptaculum seminis present.

Immature stages. Unknown.

Geographical distribution. This species is only known from medium elevations of central (Pi-lu-shih area of the Central Cross Highland Highway) (Chun-Lin LI, pers. comm. 1997) and southern Taiwan (Fig. 5).

Habitat. The type locality is located in the “Shuan-Guei-Hu Wildlife Habitat”, which is managed by the Taiwan Forestry Bureau. Elevation of the whole area ranges from 800 to 2772 m, and the climate of the habitat is quite humid, cloudy and cool. The vegetation type of the type locality is a mixture of temperate deciduous forest and subtropical evergreen forest where the following plants are dominant: *Rhododendron formosanum* HEMSL. (Ericaceae), *Illicium arborescens* HAYATA (Illiciaceae), *Osmanthus lanceolatus* HAYATA (Oleaceae), *Pasania kawakamii* (HAYATA) SCHOTT., *Castanopsis carlesii* (HEMSL.) HAYATA, *Cyclobalanopsis longinix* (HAYATA) SCHOTT. var. *kuoi* (NAKAI) LIAO (Fagaceae), *Gordonia axillaris* (ROXB.) DIETR., *Schima superba* GARDN. & CHAMP., *Camellia caudate* WALL. (Theaceae), *Phoebe formosana* (HAYATA) HAYATA, *Persea kunishii* HAYATA, *Neolitsea konishii* (HAYATA) KANEHIRA & SASAKI, *Cinnamomum micranthum* (HAYATA) HAYATA, *Beilschmiedia erythrophloia* HAYATA, *Lindera communis* HEMSL. (Lauraceae), *Clerodendrum trichotomum* THUNB. (Verbenaceae), *Wendlandia uvariifolia* HANCE (Rubiaceae), *Symplocos cochinchinensis* (LOUR.) MOORE subsp. *laurina* (RETZ.) NOOT. (Symplocaceae), *Viburnum furcatum* BLUME ex MAXIM. (Caprifoliaceae), *Alniphyllum*



Colour plate, Fig. 1: Adults of *Soritia* species. Fig. A: *S. azurea* sp. nov., ♂, holotype, upperside. Fig. B: ditto, underside. Fig. C: ditto, ♀, paratype, upperside. Fig. D: ditto, underside. Fig. E: *S. proximarginata* (PROUT), ♂, holotype, upperside. Fig. F: ditto, underside. Fig. G: A ♀ specimen of an unknown species, upperside. Fig. H: ditto, underside. Fig. I: *S. elizabetha* WALKER, ♂, upperside. Fig. J: ditto, underside. Fig. K: ditto, ♀, upperside. Fig. L: ditto, underside. — Scale refers description.

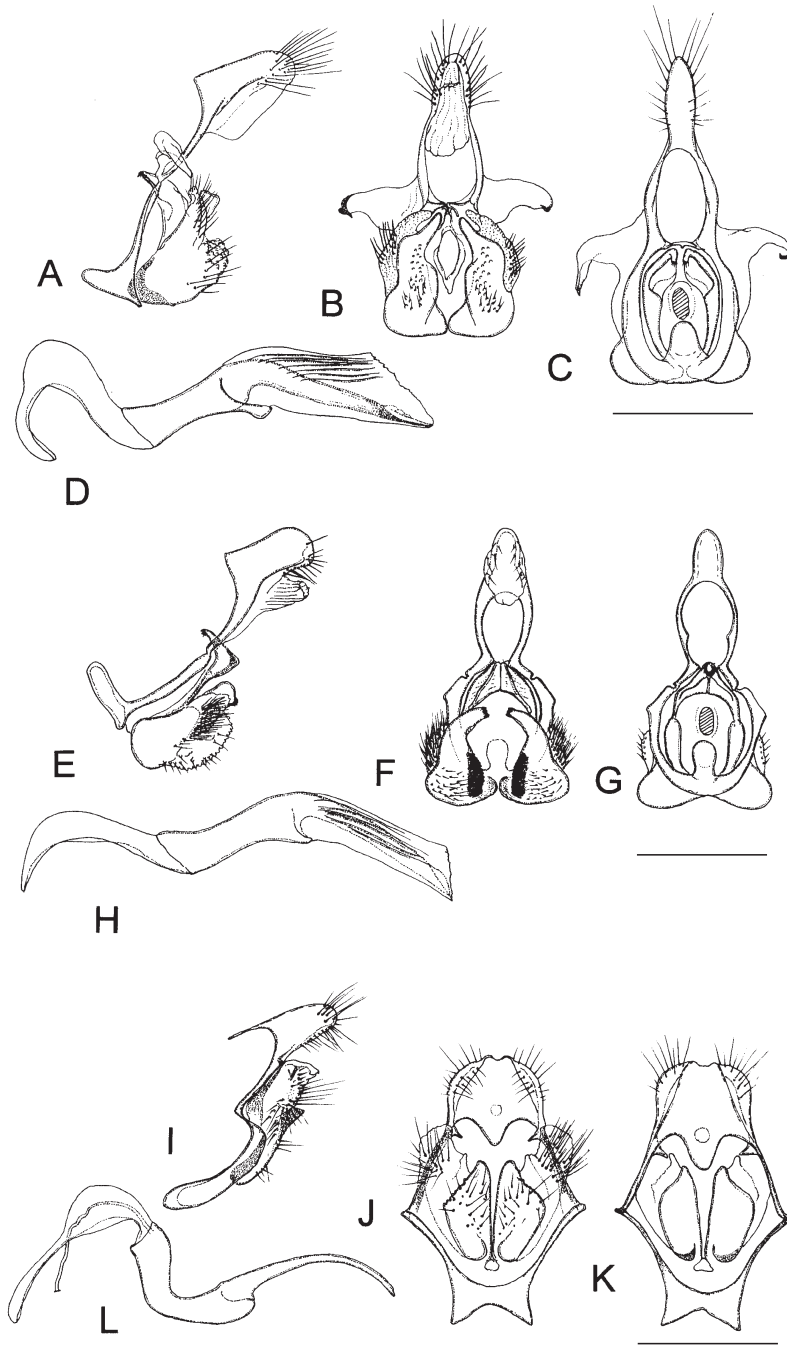


Fig. 2: ♂ genitalia of *Soritia* species. Figs. A–D: *S. azurea* sp. nov. Figs. E–H: *S. elizabetha*. Figs. I–L: *S. proprimarginata*. — Figs. A, E, I: Lateral view. Figs. B, F, J: Posterior view. Figs. C, G, K: Anterior view. Figs. D, H, L: Phallus. — Scale bar = 1 mm.

pterospermum MATSUM. (Styracaceae), *Aralia decaisneana* HANCE (Araliaceae), *Syzygium formosanum* (HAYATA) MORI (Myrtaceae), *Lagerstroemia subcostata* KOEHNE (Lythraceae), *Sloanea formosana* LI (Elaeocarpaceae), *Turpinia ternata* NAKAI (Staphyleaceae), *Daphniphyllum himalaense* (BENTH.) MUELL.-ARG. subsp. *macropodium* (MIQ.) HUANG (Daphniphyllaceae), *Prunus phaeosticta* (HANCE) MAXIM., *Prunus campanulata* MAXIM. (Rosaceae), *Ulmus uyematsui* HAYATA (Ulmaceae), *Engelhardtia roxburghiana* WALL. (Juglandaceae), *Calocedrus formosana* (FLORIN) FLORIN (Cupressaceae) and *Pinus taiwanensis* HAYATA (Pinaceae).

Biological notes. At the type locality, the new species is sympatric with *S. pulchella strandi* KISHIDA, 1995, and their behaviors are similar. The type specimens were collected around a blooming Ebenaceae tree along the

roadside. Phenology of the species is not yet clear. The larvae of *Soritia* are polyphagous on various families of vascular plants (TREMewan 1960, TARMANN 1992b, YEN & YANG 1998, and see ROBINSON et al. 2001), while in general, Symplocaceae, Theaceae, Melastomataceae, Polygonaceae and Rosaceae are more likely selected by the ♀ and accepted by the larvae.

Remarks. The new species seems to be most similar to “*Eterusia proprimarginata*” sensu ENDO & KISHIDA (1999). Having examined the holotype of *S. proprimarginata* PROUT (*Eterusia proprimarginata*, ♂, type, PROUT, [China, Hubei Province], Chang YANG, A. E. PRATT Coll., July 1888, JOICEY Bequest, Brit. Mus. 1934-120, B.M.N.H.-(9) 1.312; transferred to *Soritia* by YEN 2003b [see Figs. 1C–D]), the species illustrated by ENDO & KISHIDA (1999) obviously represents an undescribed species, and the true *S.*

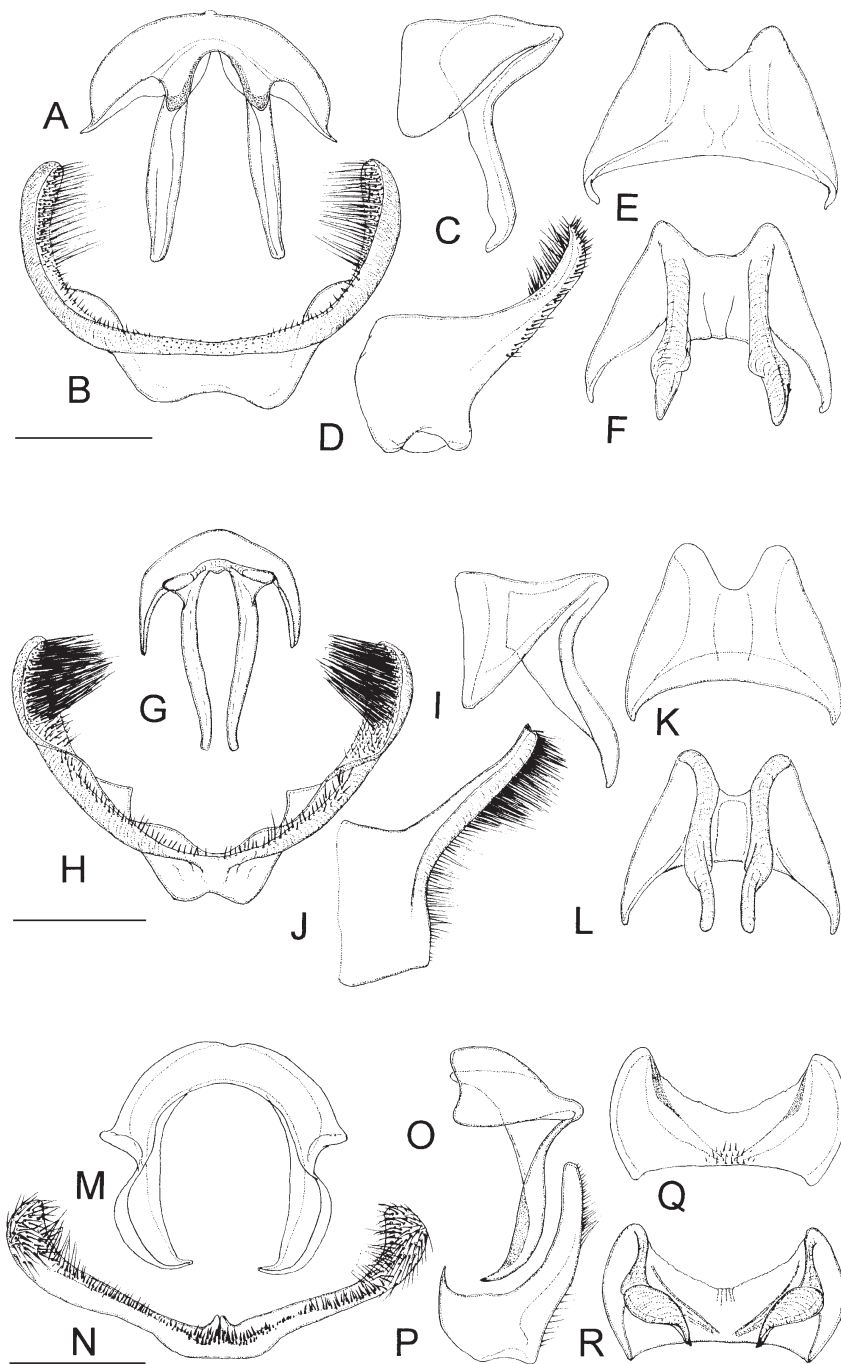


Fig. 3: Pregenital (eighth) abdominal segment of *Soritia* species. Figs. A–F: *S. azurea* sp. nov. Figs. G–L: *S. elizabetha*. Figs. M–R: *S. proprimarginata*. — Figs. A, G, M: Posterior view of tergite. Figs. C, I, O: Lateral view of tergite. Figs. E, K, L: Dorsal view of tergite; F, L, R: Ventral view of tergite. Figs. B, H, N: Posterior view of sternite. Figs. D, J, P: Lateral view of tergite. — Scale bar = 1 mm.

proprimarginata resembles examples of the *S. pulchella*-group. However, the ♀ of the true *S. proprimarginata* is still unknown. Although two specimens from Ichang (PRATT Coll., Aug. 1888) (Figs. 1G–H) have been assigned as ♀♀ of this species, and associated with the ♂ holotype in the main collection of BMNH, genitalic characters of these “inferred females” suggest that they are distant from the *S. pulchella*-group, but much closer to *S. elizabetha*, and very likely belong to another undescribed species from central China.

While checking through the whole Zygaenidae collection in BMNH, a ♀ *Soritia* which bears the same labels as the holotype of *S. proprimarginata* was found. This specimen possesses red patagia, which are characteristic for the *S. pulchella*-group. However, this feature is not sufficient to corroborate its identity and link it to the male of *S.*

proprimarginata. The species of the *S. pulchella*-group are notorious for their colour polymorphism and sympatry, which have caused great difficulties in their taxonomy (HORIE et al. 2000). The ♀ presently associated with *S. proprimarginata* and the true ♀ of *S. proprimarginata* are yet to be verified.

Discussion

The conventional concept of *Soritia* includes about two dozen species which exhibit similar phenotypic syndromes in wing pattern, e.g., narrower forewings, a continuous or interrupted medial band across the discoidal cell and approximating to the hind margin of the forewing, and a dark or brightly coloured zone from the outer margin to the postmedial line of the hindwing. This

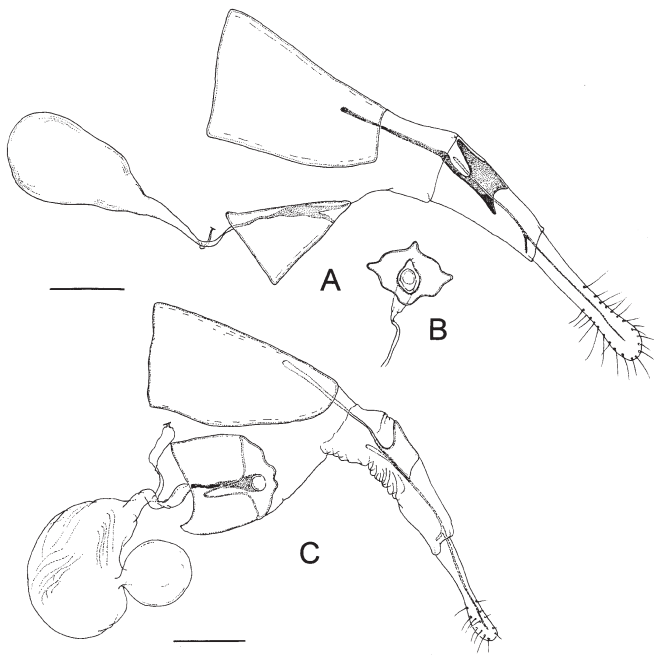


Fig. 4: Female genitalia of *Soritia* species. Fig. A: *S. azurea* sp. nov. Fig. B: ditto, ostium bursae. Fig. C: *S. elizabetha*. — Scale bar = 1 mm.

type of wing pattern is shared with *Eterusia* HOPE, 1841, another “wastepaper-basket genus” which seems to be distinguishable from *Soritia* only by its larger size (30–45 mm in forewing length) and weaker sexual dimorphism.

Since the present new species exhibits several characters unusual in the genus, a preliminary morphological study was performed to clarify its phylogenetic relationships.

In YEN (2003a), the present composite of *Soritia* was roughly separated into eight species-groups, viz.

1. *pulchella*-group (*pulchella* (KOLLAR, [1844] 1848) (sensu lato), *proprimarginata* (PROUT, 1918), *zelotypia* HERING, 1922, *terioides* (MELL, 1922));
2. *elizabetha*-group (*elizabetha* (WALKER, 1854), *choui* YEN & YANG, 1998);
3. *shahama*-group (*shahama* (MOORE, 1865), *lacreuzei* (OBERTHÜR, 1910), *lydia* OBERTHÜR, 1923);
4. *costimacula*-group (*costimacula* AURIVILLIUS, 1894, *semiflava* TALBOT & JOICY, 1922);
5. *circinata*-group (*circinata* (HERRICH-SCHÄFFER, 1854));
6. *bicolor*-group (*bicolor* (MOORE, 1884), *nigribasalis* HAMPSON, 1892, *viridibasalis* (DUDGEON, 1905));
7. *moerens*-group (*moerens* (OBERTHÜR, 1910); and
8. *sevastopuloi*-group (*sevastopuloi* TREMEWAN, 1959).

Genitalic and scent organ structures suggest that the latter four species-groups are less related to the former and *S. azurea*. The presence of androconial bristles on the hindwing and a sharp ventral process on the valva indicate a closer affinity amongst *S. circinata* (currently transferred to *Pidorus* by HORIE & OWADA 2002), *Pidorus* WALKER, 1854 and *Hemiscia* JORDAN, 1907. The *S. bicolor*-group exhibits a rather long and slightly looped bulbous ejaculatorius, which is not observed from any other species-group of *Soritia*, but shared by *Erasmia* HOPE, 1841, *Amesia* DUNCAN [& WESTWOOD], 1841 and *Pseudoscaptisyle* HERING, 1922. The dull-coloured *S.*

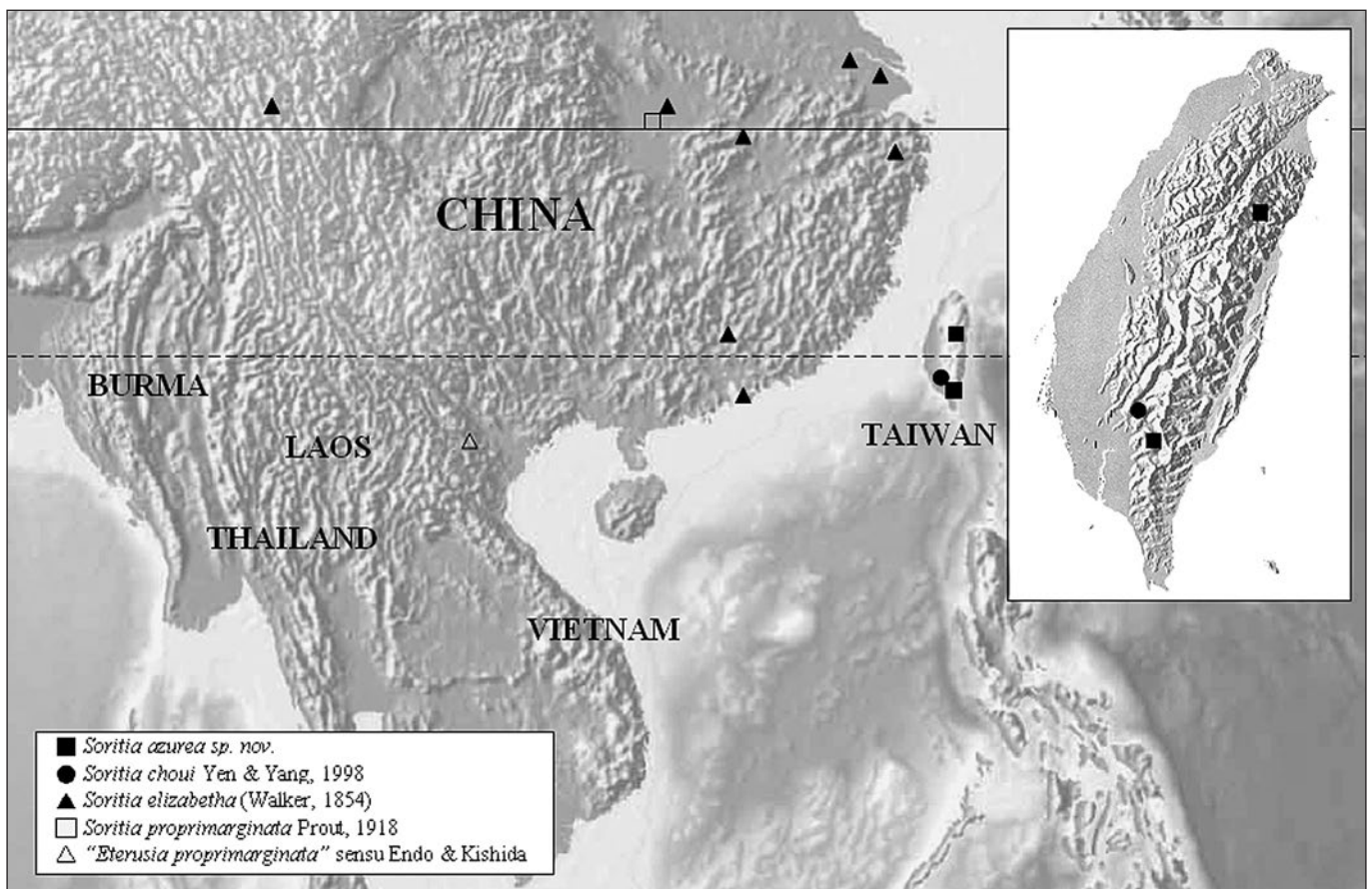


Fig. 5: Distribution map of *Soritia* species.

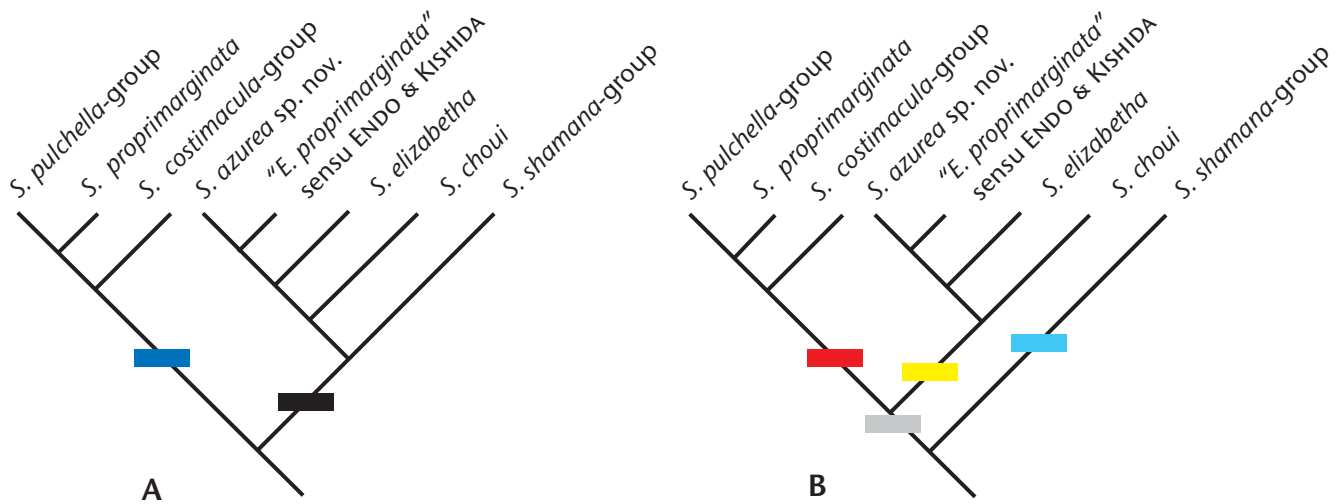


Fig. 6: Two hypotheses of inter-species group relationships of *Soritia sensu stricto* based on copulatory structures (A) and colour patterns (B). ■ “pulchella” form; ■ “elizabetha” form; ■ sexually dimorphic with “yellow female”; ■ not sexually dimorphic; ■ patagia red; ■ patagia yellow.

moerens is more related to *Milleria okushimai* OWADA & HORIE, 1999, a *Delias* butterfly mimic species belonging to the clade composed of *Chalcosia* HÜBNER, [1819] 1816, *Milleria* HERRICH-SCHÄFFER, [1853] 1850–1858, *Pseudonyctemera* PIEPERS & SNELLEN, 1903, *Psaphis* WALKER, 1854 and *Eusphalera* JORDAN, 1907.

As to *S. sevastopuloi*, it is far distant from any of the above, but resembles *Hampsonia* SWINHOE, 1894 and *Herpidia* BRYK, 1956 in the “general” shape of the ♂ genitalia, and the complex apodemal system at base of the tegumen.

When these four groups are excluded, the remaining *Soritia* species and *S. azurea* seem to be more closely related by sharing the following three character states:

1. Posterior margin of the eighth tergite in male incised medially, folded inwardly with a pair of hooks extended downwards;
2. valvae rather short, disk-like, fused at base, costal part greatly reduced and membranous;
3. ostium surrounded by strongly sclerotized lamella antevaginalis.

The morphology of the copulatory structure (♂ genitalia and pregenital abdominal segment) can be further separated into two forms: (1) the “pulchella” form (applicable to the *S. pulchella*- and *S. costimacula*-groups and *S. proprimarginata*) – uncus + tegumen-complex (= socii sensu HORIE & OWADA 2002) broad and wide dorsally, saccus angulate laterally and ventrad to base of vinculum, articulation between tegumen and vinculum angulate, m4 muscle attached on a short apodeme arising near the base of tegumen, caudal part of aedeagus slender, medial part of phallus more curved, tergal hooks more compressed laterally with apexes curved inwardly (Figs. 2I–L, 3M–R); and (2) the “elizabetha” form (applicable to the *S. elizabetha*- and *S. shahama*-groups, *S. azurea* and “*Eterusia proprimarginata*” sensu ENDO & KISHIDA) – uncus + tegumen-complex narrow and attenuate near base,

saccus swollen and extended anterodorsally, articulation between tegumen and vinculum not angulated, but accompanied with a weakly sclerotized lateral process, m4 muscle attached on a complex apodeme extended from base of tegumen and running down to base of valva, caudal part of aedeagus more straight, with an angulated process at base, medial part of phallus less curved, tergal hooks slender and more straight (Figs. 2A–H, 3G–L).

According to the above comparison, copulatory structures seem unequivocally to support two monophyletic clades within the genus (Fig. 6A), however, the colour patterns may produce another grouping (Fig. 6B). Amongst these species, the *S. pulchella*-, *S. costimacula*-, *S. elizabetha*-groups, *S. azurea* and “*E. proprimarginata*” sensu ENDO & KISHIDA are sexually dimorphic, but not the *S. shahama*-group. Except for two subspecies of *Soritia costimacula*, whose two sexes have not been well matched, the ♀♀ of sexually dimorphic species are all very similar in appearance, with yellow ground colour on all wings with several obscure spots on m_2 , m_3 and cua_1 cells. Such “yellow” ♀♀ can be further divided by the colour of patagia: (1) “Red” form in the *S. pulchella*- and *S. costimacula*-groups; and (2) “Yellow” form in the *S. elizabetha*-group, *S. azurea* and “*Eterusia proprimarginata*” sensu ENDO & KISHIDA.

Therefore, the sister group relationships of (*S. elizabetha*-group + (*S. azurea* + “*E. proprimarginata*” sensu ENDO & KISHIDA) in the above two hypotheses would lead to two different interpretations of character evolution. In the hypothesis shown in Fig. 6A, “sexual dimorphism” is synapomorphic for the whole genus while the “non-sexual dimorphism” of the *S. shahama*-group would become a derived trait. In contrast, the hypothesis in Fig. 6B gives precedence of colour patterns over copulatory structure, thus the similarity in ♂ genitalia and pregenital abdominal segment between (*S. elizabetha*-group + (*S. azurea* + “*E. proprimarginata*” sensu ENDO & KISHIDA) and *S. shahama*-group would be convergent.

The clade that includes *S. azurea* has three lineages with unsolved relationships. *S. azurea* shares rounded wings and a metallic blue sheen in the male with "*E. proprimarginata*" sensu ENDO & KISHIDA. The rounded wing shape is observed from *S. choui* YEN & YANG, 1998 as well, but the transverse stripes in the forewing of its ♀ are not present in other species. *S. elizabetha* (Figs. 1I-L, 2E-H, 3G-L) is also related to *S. azurea* based on similarity of copulatory structures and part of the wing patterns, but its elongate wing shape may put it apart from the other three members. Additionally, the similarity in ♂ genitalia between *Soritia sensu stricto*, and the *Eterusia tricolor*- (see OWADA 1992, 1996, OWADA & HORIE 1999) and *E. subcyanea*-groups needs further study to determine whether it is convergent or homologous.

As stated by YEN (2003b) (and see above), different character sets may possibly produce incompatible classifications. A comprehensive study which uses all the available character sets from different stages is needed to provide a well-supported phylogeny upon which a sound classification can be based.

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