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Rediscovery of *Heliophorus yunnani* D'Abrera and Its Systematic Position with Intrageneric Relationship in the Genus *Heliophorus* (Lepidoptera: Lycaenidae)*

Masaya YAGO[1,**], Toyohei SAIGUSA[1] and Akinori NAKANISHI[2]

[1]*Biosystematics Laboratory, Graduate School of Social and Cultural Studies, Kyushu University, 4–2–1 Ropponmatsu, Chuo-ku, Fukuoka, 810–8560 Japan*
[2]*Institute of Nature and Environmental Sciences, Himeji Institute of Technology, Yayoi-ga-oka 6, Sanda, Hyogo, 669–1546 Japan and Division of Phylogenetics, Museum of Nature and Human Activities, Hyogo, Yayoi-ga-oka 6, Sanda, Hyogo, 669–1546 Japan*

Abstract. A lycaenid butterfly, *Heliophorus yunnani* D'Abrera, was rediscovered since its first capture 78 years ago in the subalpine zone of NW Yunnan, China. Both adult male and female of this species are morphologically investigated in detail. A new systematics of the genus *Heliophorus* Geyer is proposed. *H. yunnani* is included in its own group within the subgenus *Kulua* Zhdanko.

Key words: *Heliophorus yunnani,* Lepidoptera, Lycaeninae, *Heliophorus,* morphology, systematics.

Introduction

A lycaenine butterfly, *Heliophorus yunnani,* was described by D'Abrera (1993) based on unstated number of specimens including at least each two illustrated specimens of both sexes, which were found in M. G. Mansfield's collection of butterflies in the British Museum (N. H.) (now The Natural History Museum). These butterflies were brought by a British botanist, G. Forrest, who extensively surveyed Yunnan, China early in this century. The collecting data of the type material simply stated "Yunnan, 1918", and no further information on the type locality of this species is known. This was the same case for *Bhutanitis mansfieldi* (Riley, 1939) of which the type was also in the collection of Mansfield. Although rich materials of many Chinese butterflies recently have been brought to Japan and Europe, no additional material of *H. yunnani* has been recorded. Therefore this species seems to be very rare or extremely local in distribution.

In June of 1996, one of us, Saigusa, and other members of a project surveying the insect fauna of Yunnan collected some butterflies belonging to a lycaenid species which had unique markings on the underside of the wings. These butterflies were found only along narrow grasslands bordering the upper limit (about 3,000 m alt.) of the summer-green forest of Habaxueshan in NW Yunnan, China. They are quite identical with butterflies illustrated in D'Abrera (1993) as *Heliophorus yunnani.* This is the first record of the species since its discovery 78 years ago.

D'Abrera (1993) described wing markings of this species in detail, and stated that its peculiarity in the size, marking and shape of the wings, including the absence of the hindwing tail made it unique within the genus *Heliophorus* Geyer, 1832. In addition to this peculiarity in general appearance, this species was found in biotope situated at the border between the cool temperate deciduous forest and the subalpine coniferous forest. This habitat is quite different from those of all congeners of the genus *Heliophorus,* which are found in and around subtropical and tropical forests in the Oriental Region.

As stated above, *H. yunnani* is much different from other *Heliophorus* species. However, no structural characters of this butterfly were investigated by D'Abrera, and no reasons for including it in *Heliophorus* were given. In this paper we verify the generic assignment of this butterfly, and discuss its phylogenetic position based on external morphology, especially the structure of the genitalia and the wings of both sexes.

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** E-mail: yagorcb@mbox.nc.kyushu-u.ac.jp

The systematics of *Heliophorus* was first extensively worked by Riley (1929) based on the characters including the male genitalia. Eliot (1973) and Sibatani (1974) gave important contributions to the generic classification of the subfamily Lycaeninae to which *Heliophorus* belongs. The most recent work is that of Zhdanko (1995), who divided *Heliophorus* into two genera, *Heliophorus* and *Nesa* Zhdanko, 1995, and further divided *Heliophorus* into two subgenera, *Heliophorus* and *Kulua* Zhdanko, 1995, based on the markings of the forewing underside, and genitalia of both sexes, etc. We also make comments on his classification.

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Materials and Methods

The following specimens of *Heliophorus* were examined. Half of the specimens from China collected by the expeditions cooperated with the Kunming Institute of Zoology are deposited in the collection of that Institute.

H. yunnani: 6♂3♀, Tuomunan (3,030 m), 42 km N of Qiaotou, Habaxueshan, Yunnan, China, 9 June 1996 (T. Saigusa, T. Naito & T. Yagi col.). *H. tamu*: 1♂1♀ (Nepal); 2♂ (Sikkim); 2♂ (N. Burma). *H. brahma*: 4♂1♀ (Assam); 2♂ (N. Burma); 6♂2♀ (Laos); 2♂ (Tam dao, N. Vietnam); 3♂3♀ (Sichuan, China); 3♂2♀ (Yunnan, China). *H. androcles*: 36♂ 19♀ (Nepal); 4♂ (Sikkim); 2♂ (Assam); 7♂1♀ (Bhutan). *H. viridipunctata*: 1♂ (N. Burma); 1♀ (Thailand); 4♂3♀ (Sichuan, China); 4♂6♀ (Yunnan, China). *H. moorei*: 8♂1♀ (N. Burma). *H. saphirioides*: 2♂ (Yunnan, China). *H. oda*: 2♂ (Nepal). *H. saphir*: 8♂8♀ (Sichuan, China); 2♂1♀ (Zhejiang, China). *H. epicles*: 12♂4♀ (E. Java); 21♂8♀ (Malaya); 3♂ (Thailand); 4♂6♀ (Laos); 1♂1♀ (Hainan); 1♂ (Yunnan, China); 4♂3♀ (Assam); 10♂ 2♀ (Nepal). *H. ila*: 2♂ (Malaya); 3♂ (Thailand); 1♂ (Laos); 4♂3♀ (Sichuan, China); 2♂ (Yunnan, China); 58♂29♀ (Taiwan). *H. kohimensis*: 2♂ (Assam); 22♂ 3♀ (N. Vietnam); 1♂ (Yunnan, China). *H. indicus*: 2♂ (Nepal); 2♂ (Assam). *H. kiana*: 7♂5♀ (Kina-Balu, N. Borneo).

The structures for integumental morphology were macerated with 15% KOH, and examined under a binocular microscope with magnification up to ×126.

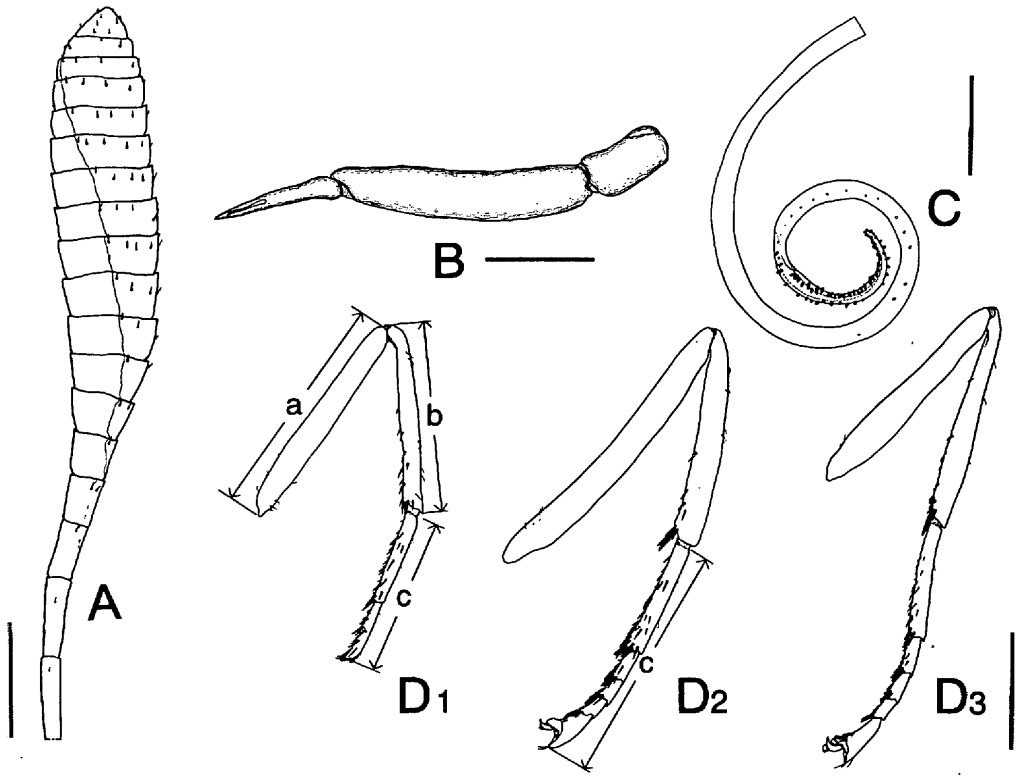

Fig. 1. External structures of *Heliophorus yunnani* ♂. A: Right antenna terminal 18 segments, dorsal aspect. B: Left labial palpus, lateral aspect. C: Probosis, lateral aspect. D_1–D_3: Left legs, lateral aspect. D_1: Foreleg. D_2: Midleg. D_3: Hindleg. a, length of femur; b, length of tibia; c, length of tarsus. Scales A, 0.5 mm; B, 0.5 mm; C, 0.5 mm; D, 1.0 mm.

Results

I. Morphological description of *Heliophorus yunnani*

Head

Vestiture: Vertex, occiput and frontoclypeal area covered with many fulvous long hairs and several white and black hairs; frontoclypeal area covered with compact white scales along eye margin; occiput clothed with white hairs and scales along posterior margin of eye.

Labium clothed with long white hairs, mixed with white and some black scales. Labial palpus covered with black and several white scales above on apical half of 2nd segment and 3rd segment, roughly clothed ventrally with long white and black hairs on 1st and 2 nd segments. Chaetosema slightly swollen, with dense brown hairs. Antenna black-scaled, with basal portions of flagellomeres white-scaled; club black-scaled anteriorly, white-scaled posteriorly; nudum dark. Cranium black. Compound eye bare. Antenna almost half as long as forewing costa, slightly longer than discoidal cell, consisting of 33–34 segments; club weakly flattened, consisting of 15 segments; nudum expanded from base to tip of club, widened apically and entirely occupying apical two segments, and spinules arranged in 6 rows more or less irregular in middle of club and reduced to 1–2 rows at basal segments of club. Proboscis black, with 60–65 sensilla styloconica on apical portion, flower-like in shape, arranged in anterior and posterolateral rows, with sensilla alternately directed. Length of antenna: ♂; 7.8–8.3 mm. ♀; 7.0–7.4 mm.

Thorax

Vestiture and coloration. Sclerotized portion black. Nota clothed with long greyish hairs, pleura with white hairs, upper portion clothed in white and some black hairs. Integument of legs brown, covered with white scales, mixed with black hairs particularly on dorsal surface of tibiae; femora clothed with long white hairs below; tarsi white-scaled, and annulated with black scales at tips of each tarsomere, annulation indistinct in male.

Femora long, slender and bare. Tibiae sparsely clothed with spines posterolaterally below middle; mid and hind tibiae with pair of terminal spurs. Tarsi densely covered with spinules ventrally. Claws of same length, curved ventrally, uncinate at apex. Lengths of leg segments of male are given in Table 1.

Table 1. Mean lengths (mm) of male leg segments of *H. yunnani*. (n=6) (See Fig. 1).

	Femur	Tibia	Tarsus
Foreleg	1.99	1.69	1.51
Midleg	2.71	1.93	2.16
Hindleg	2.22	2.07	2.36

Wing

Wing shape

♂: Forewing almost triangular in shape; costa much weakly curved, more or less arched near base; apex rather pointed; termen almost straight, only slightly arched; hind margin almost straight. Hindwing rounded; costa almost as long as inner margin; termen strongly and evenly rounded, neither produced at tip of vein 6 nor dentate at tips of veins; tail absent and anal lobe undeveloped. Length of forewing: 1.55–1.61 mm.

♀: Similar to male, but forewing termen strongly rounded, relative length of costa to hind margin shorter, so that apex more weakly produced and rounded. Length of forewing: 1.42–1.53 mm.

Wing venation

Venation similar to other species of *Heliophorus*. Forewing discoidal cell half as long as wing, with discocellulars slightly oblique to costa, so that pos-

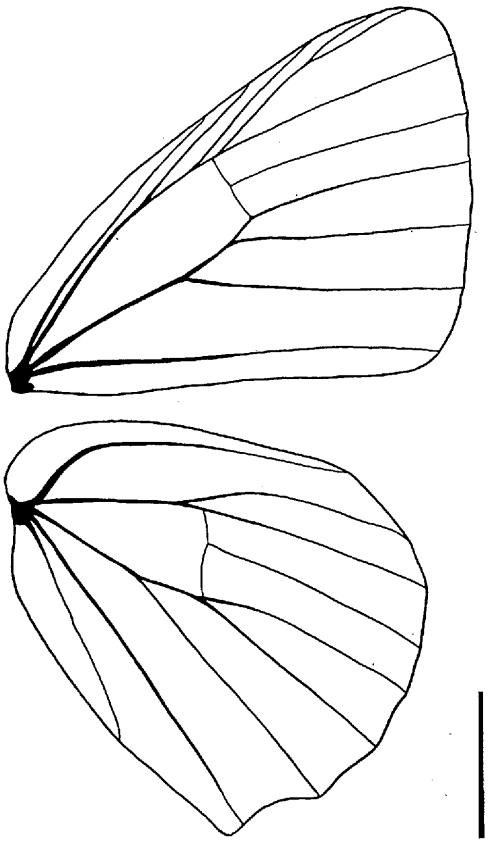

Fig. 2. Wing venation of *Heliophorus yunnani* ♂. Scale bar=4.0 mm.

terodistal corner of discoidal cell slightly obtuse; vein 12 ending slightly before discocellulars; veins 6 and 9 arising from point or short stalk; common stem of veins 7 and 9 slightly longer than vein 7; cell 2 nearly as wide as cell 1b+c at termen.

Hindwing discoidal cell evenly widened apically, with upper and lower discocellulars almost aligned perpendicular to costa, and posterodistal corner acute; veins 3 and 4 arising from posterodistal corner of discoidal cell; base of vein 7 close to but distinctly separated from that of vein 6; vein 7 divergent from vein 6 at basal portion, then almost parallel with latter.

Wing marking

As to the nomenclature of underside markings of the wings we adopted the system proposed by Schwanwitsch (1949) in the following description.

♂: Upperside of forewing purplish-blue with dim lustre, with narrow costal and broad black outer marginal borders; outer marginal border distinctly expanded towards apex, and angulately produced into bluish area at veins 2 to 4; width and relative width of black border to cell 1b+c width at outer margin 1.17–1.65 mm and 0.65–0.87 in cell 1b+c, 2.13–2.70 mm wide and 1.18–1.42 in cell 2, 2.58–3.05 mm wide and 1.43–1.61 in cell 3, 2.99–3.53 mm wide and 1.66–1.85 in cell 4, 3.28–3.73 mm wide and 1.82–1.96 in cell 5, 3.86–4.23 mm wide and 2.14–2.23 in cell 6, and 4.40–4.70 mm and 2.44–2.47 at apex. Fringe consisting of basal short black scales and apical long greyish-white scales, latter slightly darker at tips of veins 2 and 3.

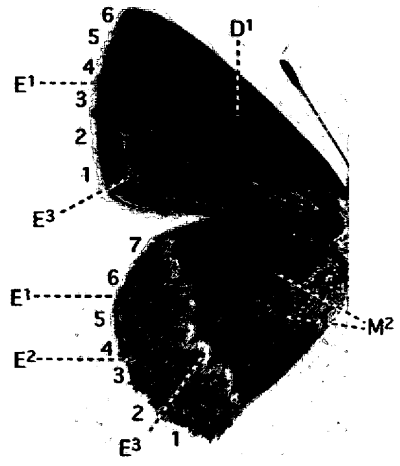

Fig. 3. Wing markings of *Heliophorus yunnani* interpreted by the terminology by Schwanwitsch (1949).

Upperside of hindwing extensively purplish-blue as in forewing, and with broad outer marginal border nearly as wide as that in forewing cell 2; outer margin of purplish-blue area distinctly undulate, acutely produced at each vein; width of black border 2.4–2.5 mm in cell 1b+c, 1.9–2.5 mm in cell 2, 1.8–2.4 mm in cell 3, 2.3–2.8 mm in cell 4, 2.5–3.1 mm in cell 5, 3.8–4.2 mm in cell 6; reddish-orange submarginal lunules appearing in cells 1b+c and 2, and sometimes in cell 3; that in cell 1b+c expanded to tornal area.

Underside of forewing ochreous with yellow tinge in ground colour, with obscure large orange discal patch covering posterodistal part of discoidal cell and its surroundings to middle 1/2 of cell 1b+c; basal portions of cell 1a and 1b+c dark grey; most of cell 1 a whitish, but often darkened to dark grey, particularly along vein 1b+c; D^1 (discocellular bar) recognizable as an obscure fine dark line in some specimens; E^3 (inner submarginal blackish bar) sometimes appearing in cell 1b+c, bordered along both sides with white areas; the inner whitish border also appearing in cell 2 and in some specimens faintly even in cell 3; M^1 (postdiscal marking) completely absent. Fringe consisting of shorter orange scales and longer whitish ones, some of which are tinged with grey apically, and those at tips of veins 1a+b and 2 and along apical portion of posterior margin of wing blackish.

Underside of hindwing yellowish ochreous in ground colour as in forewing, with very broad pale pinkish submarginal border suffused with white scales, and bordered inwardly with series of white lunules representing part of E^3, and bordered outwardly with series of obscure, slender, white marginal stripes separated by each vein along termen; width of submarginal border 1.4–2.0 mm in cell 1a, 2.2–2.7 mm in cell 1b+c, 2.5–3.2 mm in cell 2, 2.6–3.4 mm in cell 3, 3.4–4.1 mm in cell 4, 3.5–3.9 mm wide in cell 5, 2.1–2.8 mm in cell 6, 0.78–1.1 mm in cell 7; the white lunules arranged almost parallel to termen, but slightly shifted inwardly in cells 4 and 5; width of lunule in cell 1b+

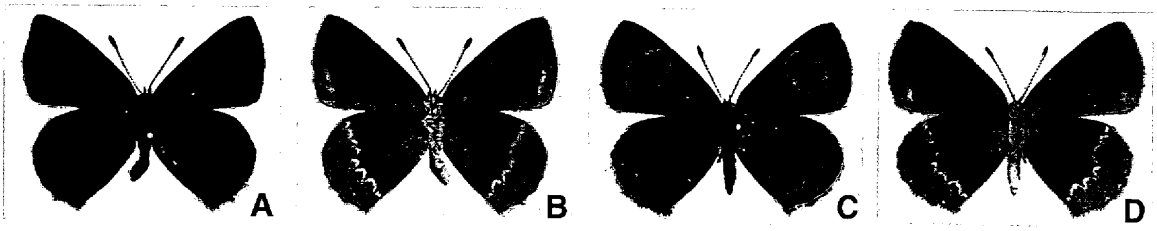

Fig. 4. *Heliophorus yunnani* D'Abrera, 1993, Habaxueshan, Yunnan, China. A: ♂, upperside. B: Ditto, underside. C: ♀, upperside. D: Ditto, underside.

c 0.38–0.40 mm; marginal white stripes along termen covering black scales which represent E1; small to minute black dot representing M^2 appearing in cell 1b +c and discoidal cell; M^1 completely disappearing. Fringe almost as in forewing, but longer scales becoming darker towards tornus.

♀: Upperside of forewing blackish brown, with large, orange, elliptical discal patch expanding from vein 11 to cell 1b+c, 6.43–7.06 mm in transverse length, 4.05–4.31 mm in longitudinal length; orange scales scattered in distal portion of discoidal cell and basal portions of cells 1b+c and 2. Fringe consisting of shorter black scales and outer whitish scales, the latter sometimes darkened at tips of veins 1b+c and 2.

Upperside of hindwing blackish brown, with series of orange submarginal lunules from cell 1a to cell 5 (1.55–1.62 mm wide in cell 1b+c): lunules becoming smaller and more obscure towards cell 5; some orange scales scattered on veins 2 and 3. Fringe consisting of shorter blackish scales and longer whitish scales on anterior portion, and of orange scales on posterior portion.

Underside of forewing as in male, but discal orange patch wider and brighter, E^3 of cell 1b+c more distinct.

Underside of hindwing also as in male, but differing in outer marginal white stripes more clearly developed, and weakly convex inwardly.

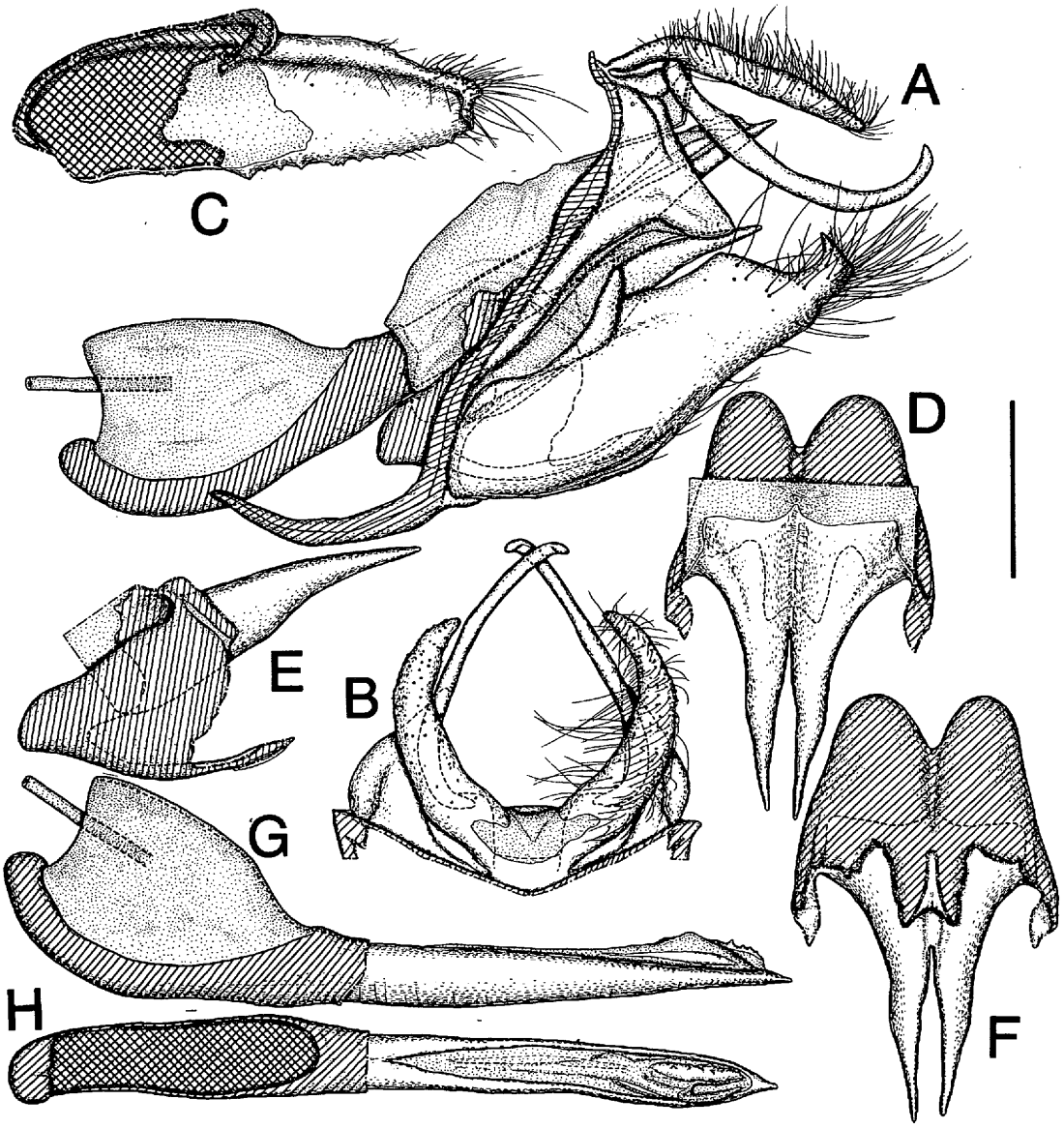

Fig. 5. Male genitalia of *Heliophorus yunnani*. A: Genitalia as a whole, lateral aspect. B: Dorsum, dorsal aspect. C: Right valva, dorsal aspect. D: Juxta, dorsal aspect. E: Ditto, lateral aspect. F: Ditto, ventral aspect. G: Phallus, lateral aspect. H: Ditto, dorsal aspect. Scale bar=0.5 mm.

Abdomen

Abdominal sclerites brown in color. Abdomen covered dorsally with brown scales and hairs, mixed with some white scales; lateral portions of 1st to 4th terga with long brown hairs; 8th tergum bearing rather stiff long brown hairs on posterior margin. Abdomen covered ventrally with white scales and hairs, mixed with some black scales. Lateral portions of 1st to 4th sterna clothed with rather long white hairs; 8th sternum bearing long white hairs.

Genitalia

Male genitalia

Rather slender as a whole. Ring inclined posteriorly, distinctly oblique to body axis, sagittal diameter 1.3×as long as high. Tegumen well developed, produced into posterolateral processes, which are moderately long, broad basally, tapered apically and extend posteroventrally to level slightly beyond middle of socius. Vinculum narrow, tapered ventrally; saccus moderately long, half as long as height of ring. Socius moderately long, half as long as height of ring, clothed with longish hairs above; in lateral aspect only slightly directed posteroventrally, evenly slender and nearly straight beyond subbasal portion; in dorsal aspect moderately broad basally, divergent from opposite socius to apical 2/3, then gently convergent, and ending in more or less tapered apex. Falx evenly slender, long, weakly curved throughout length, with tip extending rather well beyond tip of socius. Valva nearly 1.2×as long as height of ring, in lateral aspect moderately broad on basal portion, weakly narrowed to apical 3/4, then constricted to subapical portion, ending in small dorsally projecting keel; in dorsal aspect valva rather narrow and tapered at subapical portion, ending in truncate apex; valva with distinct internal ridge subbasally on dorsal half of basal margin of outer surface; ridge dividing weakly swollen distinct basal flange, lacking special projection, articulated with dorsolateral corner of juxta; dorsal margin of valva weakly keeled; ventral margin of valva straight, minutely serrate throughout. Phallus rather long, moderately thick, almost straight, 1.6×as long as height of ring; suprazonal portion slightly longer than subzonal portion, straight, gradually tapered apically, ending in short apical projection; dorsal surface of suprazonal portion of aedeagus almost entirely occupied by perivesical area; short narrow sclerite near vesical opening bearing several proximally directing denticles; subzonal portion more or less curved dorsally towards proximal end; coecum penis very short. Juxta strongly developed, nearly as long as height of ring, dorsal portion plate-like, moderately broad, flattened basally, produced into pair of very long, slender, sharply pointed processes close to

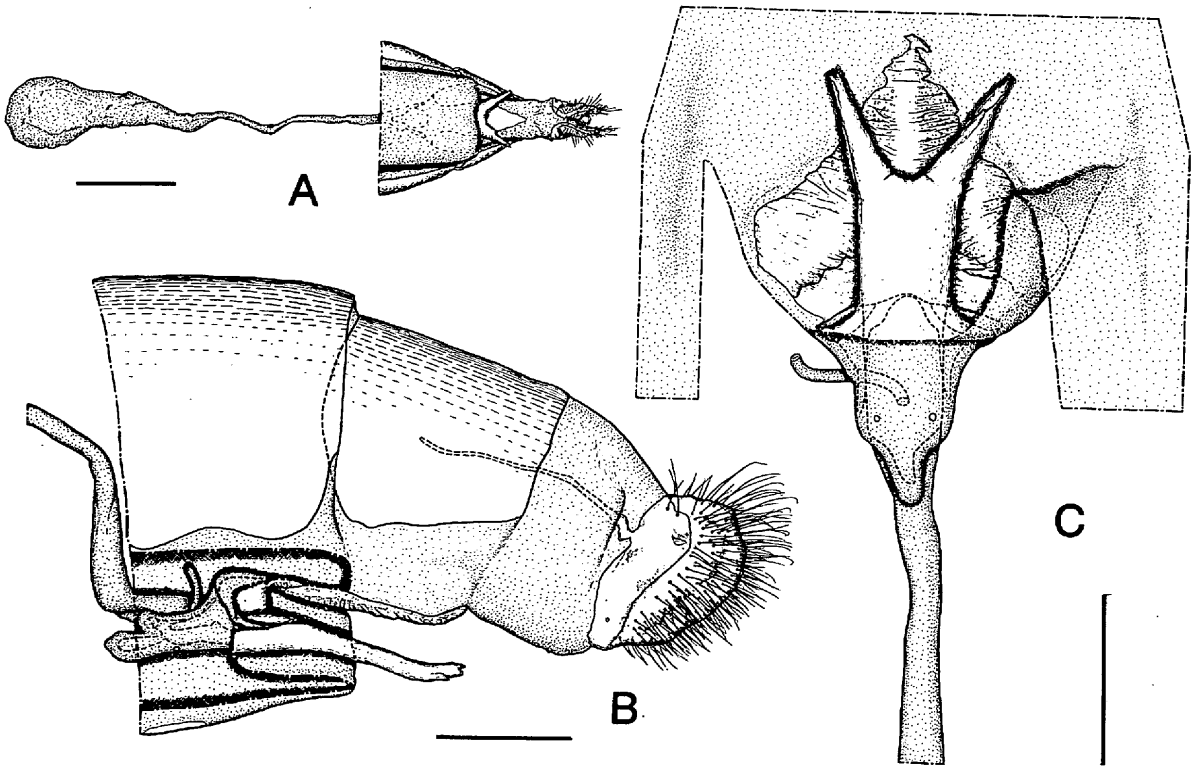

Fig. 6. Female genitalia of *Heliophorus yunnani*. A: Genitalia as a whole, ventral aspect. B: Genitalia except for corpus bursae, lateral aspect. C: Genital plate, ventral aspect. Scale bars=1.0 mm (A); 0.5 mm (B); 0.5 mm (C).

and parallel with each other; ventral portion of juxta represented by broad and deep invagination, terminating in pair of large coeca; ventromedian portion of juxta produced anteriorly into flexed projection which is tightly associated with basal portions of valvae. Length of ♂ genitalia: 2.0 mm.

Female genitalia

Eighth abdominal tergum large and trapezoidal, narrower posteriorly. Genital plate consisting of composite sclerite including ostium bursae and large cordate 8th sternum, more or less distinctly connected with each other by weak ventromedian sclerotization. Composite sclerite with obliquely vertical, mostly postvaginal basal portion surrounding ostium bursae and large free horizontal antevaginal free process completely united with each other. Free process Y-shaped, weakly curved ventrally towards tip, slightly narrower than anal papillae, as long as 8th tergum, 2.9×as long as wide, flattened slightly thicker proximally, widened at base, slightly dilated to apical 0.6, then bifurcate into rather slender, weakly tapered branches gently divergent from each other; proximal portion of free process shallowly and longitudinally concaved as furrow on dorsal surface. The basal portion of genital plate small, oval, transversely long, slightly wider than base of antevaginal process, distinctly and roundly swollen at middle portion, which is tightly pressed against furrow-like dorsal concavity of free process; lateral portions of oval portion invaginated into short funnel-like concavities. Cordate sclerite representing main part of 8th sternum flat overall, slightly shorter than 8th tergum, as long as basally wide, deeply emarginate anteriorly, pointed posteriorly, with weak transverse wrinkles. Bursa copulatrix consisting of moderately long ductus bursae and elongate corpus bursae. Ductus bursae nearly 3/5 as long as 8th tergum or antevaginal process, 2/3 as thick as wide, gently tapered distally, thick and transparent in endocuticular layer of coelomic side, more or less sclerotized and pigmented in exocuticular layer of lumen side, concaved and membranous dorsally, invaginated anteroventrally into short slender coecum, which is more or less sclerotized on luminal side (this coecum is here termed as coecum bursae; area in which apical portion of aedeagus is presumably inserted); pair of tiny dark spots on ventral side at middle. Corpus bursae long, nearly 5×as long as 8th tergum, evenly slender for posterior 1/2, arising from middle of dorsal surface of ductus bursae for 1/2 length of ductus bursae and directed dorsally, then curved anteriorly, evenly slender to middle of corpus, then rather cylindrically thickened on distal (anterior) 1/2, of which diameter is 2/3 of length of 8th tergum; no signum developed. Papilla analis oval in lateral aspect, shorter than deep, sclerotized on proximal 2/5, bearing setae of various lengths, with apophysis anterioris slightly longer than depth of papilla. Length of ♀ genitalia: bursa copulatrix (from ostium to end of corpus) 4.43 mm; lamella antevaginalis 0.80 mm.

II. Morphological diversity in the genus *Heliophorus*

It is necessary to review the morphological diversity of the adult in the genus *Heliophorus* in order to determine the systematic position of *H. yunnani*. In this section we state the results of a comparative morphological survey, based especially on the characters used by Zhdanko (1995) to divide *Heliophorus* into two subgenera. Based on our resultant classification of this genus stated in the final part of this paper,

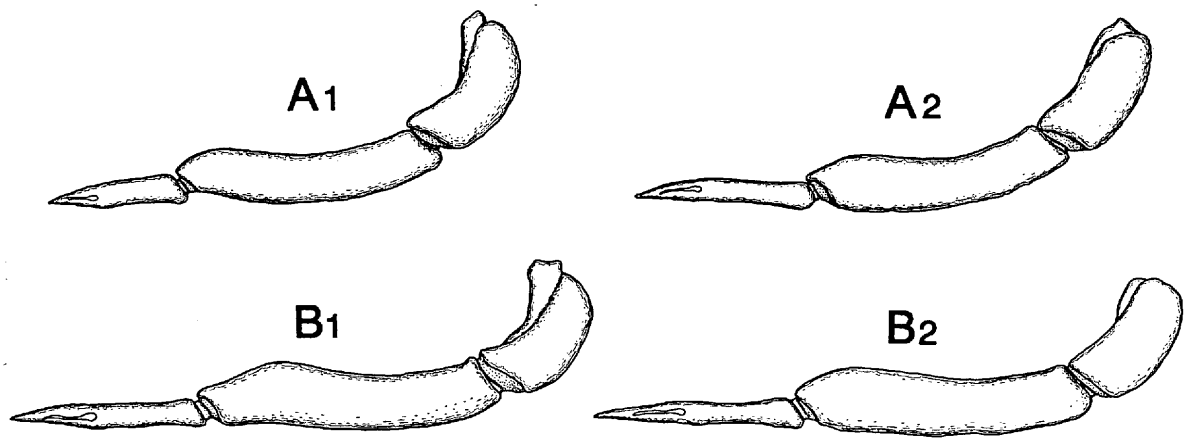

Fig. 7. Left labial palpus of species of *Heliophorus*, lateral aspect. A_1: *Heliophorus* (*Heliophorus*) *epicles*. A_2: *Heliophorus* (*Heliophorus*) *kohimensis delacouri*. B_1: *Heliophorus* (*Kulua*) *tamu*. B_2: *Heliophorus* (*Kulua*) *brahma*. Scale bar=0.5 mm.

we use two of the species group names for the following statement. The species included in these groups are as follows, the *epicles* group: *epicles, ila, kohimensis, indicus, cantliei,* the *tamu* group: *tamu, brahma, androcles, viridipunctata, moorei, saphirioides, oda, bakeri, hybrida, pulcher.*

Labial palpus

Relative lengths of the 2nd and 3rd palpomeres of the labial palpus are used as one of subgeneric characters by Zhdanko (1995). According to him the 3rd palpomere is slightly shorter than the 2nd in *Kulua.* The relative length of the 2nd palpomere to the 3rd is 1.40–1.95 in the *epicles* group, 1.6 in *kiana,* and 1.45–1.70 in the *tamu* group, and 1.55 in *saphir* (Table 2). Consequently there is no distinct difference in this character between the subgenera *Heliophorus* and *Kulua* of Zhdanko (1995).

Wing shape

The male forewing has an almost straight costa and outer margins, so that the apex is pointed in most species except *kiana,* of which the costa is rather arched and apex is not so much produced as in other species, and the male hindwing has the inner margin longer than the costa, so that the wing is elongated towards the tornal area. In *saphir,* the inner margin is almost as long as the costa, and wing is rather rounded. The outer margin of the male hindwing is always more or less distinctly undulate. The male hindwing has a tail in most species except for *bakeri.* The tail is long and slender in the *epicles* group and *saphir,* while short in the *tamu* group. In the latter group the tail is reduced to a simple dentation as in *bakeri* and *oda.* The tail of *kiana* is long and evenly broad, and characteristically curved and white-fringed throughout. The female wings are almost always more rounded than in the male owing to the shortened forewing costa and hindwing inner margin. The hindwing tail in the female of the *tamu* group is usually much longer than in the male and its length is almost equal to those in the *epicles* group.

Wing markings

1) *Upperside of male forewing*

The discal area of the upperside of the male forewing is covered with scales of metallic lustre in all species except *kiana* which is uniformly dark brown. The coloration of the discal area is variable by species.

Table 2. Relative length of 2nd palpomere to 3rd palpomere of labial palpus.

epicles group

Species (Subspecies)	*epicles*	*kohimensis* (*delacouri*)	*ila* (*matsumurae*)
Relative length	1.95	1.40	1.56

Species	*kiana*	*saphir*
Relative length	1.60	1.55

tamu group

Species	*tamu*	*brahma*	*viridipunctata*	*saphirioides*	*moorei*	*oda*	*androcles*
Relative length	1.55	1.45	1.56	1.60	1.64	1.60	1.70

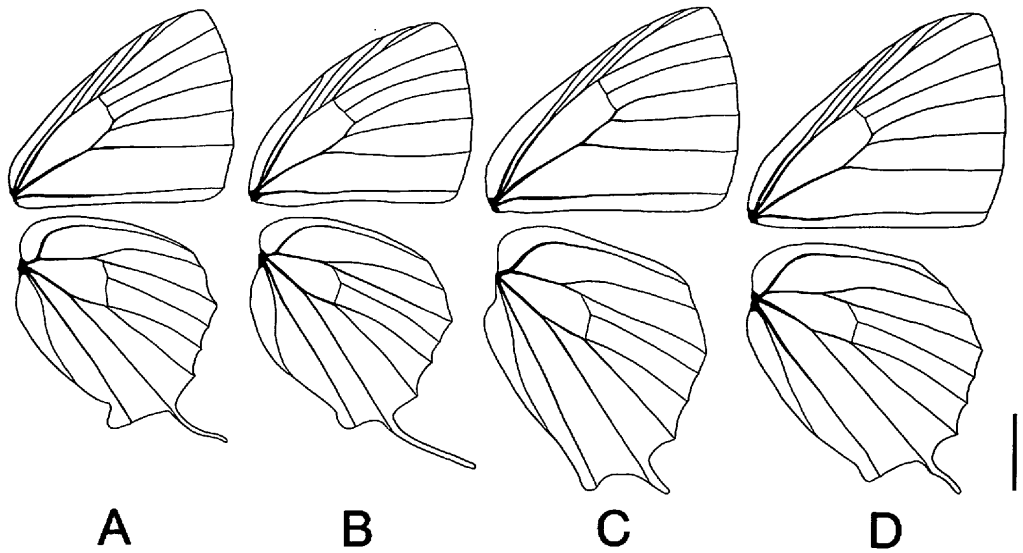

Fig. 8. Wing venation of ♂ of *Heliophorus* species. A: *Heliophorus* (*Heliophorus*) *epicles.* B: *Heliophorus kiana.* C: *Heliophorus* (*Kulua*) *tamu.* D: *Heliophorus* (*Kulua*) *saphir.* Scale bar=4.0 mm.

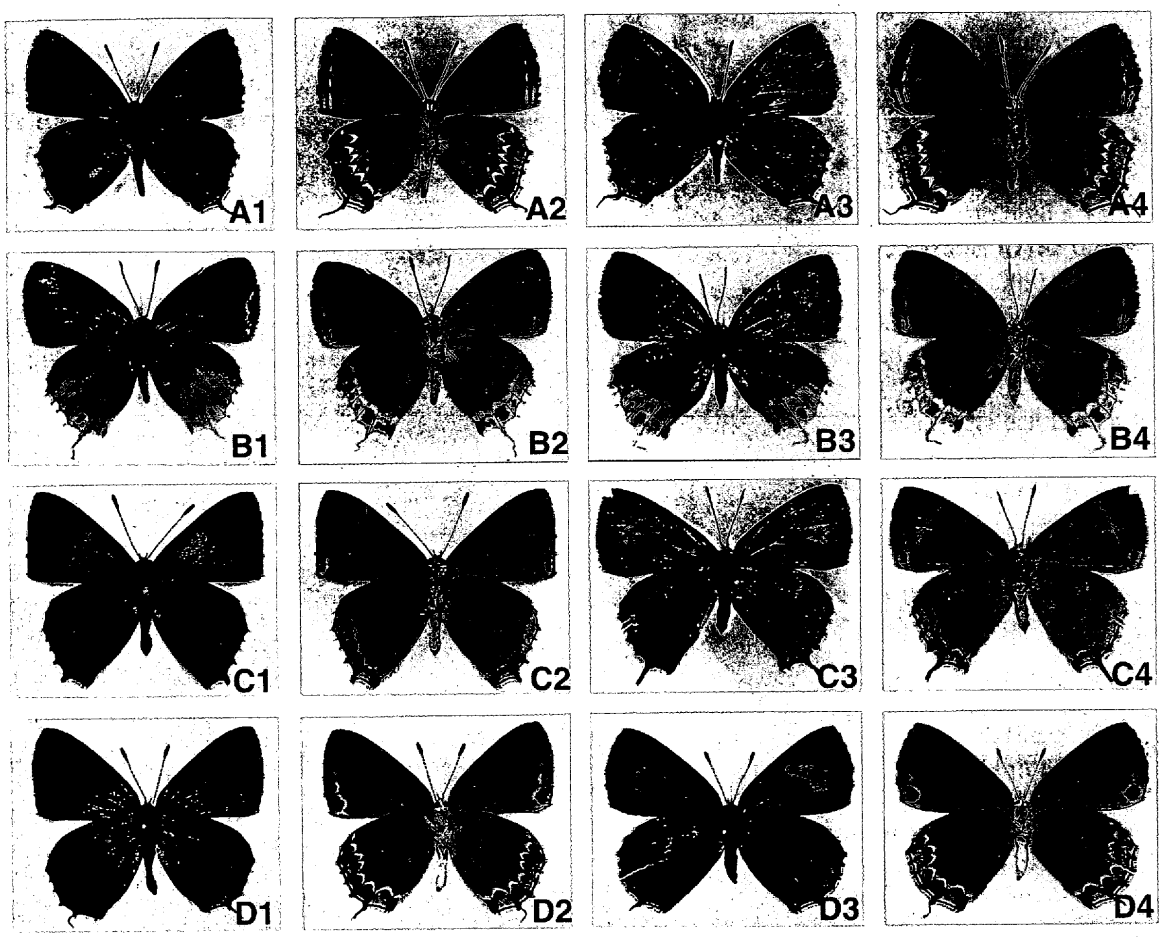

Fig. 9. The *epicles* group. A1: *Heliophorus* (*Heliophorus*) *epicles* ♂, E. Java, upperside. A2: Ditto, underside. A3: *Heliophorus* (*Heliophorus*) *epicles* ♀, E. Java, upperside. A4: Ditto, underside. The *kiana* group. B1: *Heliophorus kiana* ♂, Kina-Balu, N. Borneo, upperside. B2: Ditto, underside. B3: *Heliophorus kiana* ♀, Kina-Balu, N. Borneo, upperside. B4: Ditto, underside. The *tamu* group. C1: *Heliophorus* (*Kulua*) *tamu* ♂, N. Burma, upperside. C2: Ditto, underside. C3: *Heliophorus* (*Kulua*) *tamu* ♀, Nepal, upperside. C4: Ditto, underside. The *saphir* group. D1: *Heliophorus* (*Kulua*) *saphir* ♂, Sichuan, China, upperside. D2: Ditto, underside. D3: *Heliophorus* (*Kulua*) *saphir* ♀, Sichuan, China, upperside. D4: Ditto, underside.

It is always deep to blackish-purple in the *epicles* group, but variable in the *tamu* group; purplish to greenish-blue in *moorei, androcles, oda, saphirioides* and *bakeri,* while in *tamu* and *viridipunctata* green, and in *brahma* golden with an orange tint. The discal metallic patch usually occupies the basal 1/2 to 2/3 of the wings in most species, but it may expand to the submarginal portion in *kohimensis,* or reduced to the basal 1/3 in *viridipunctata.* In addition to the metallic marking, the orange patch often appears on the post-discal area beyond the discocellular in some races of *epicles* and *ila.*

2) *Upperside of male hindwing*

The discal area is covered with a metallic patch as in the forewing, but it usually expands to the submarginal area close to the submarginal orange lunules. In *tamu* the discal patch is much reduced, and in *viridipunctata it* almost entirely disappears. The orange lunules situated between E^2 and E^3 appear in all species except for *kiana,* although the size and position are variable by species or subspecies (*kohimensis, indicus* and *ila ila* are often obscure). In *kiana,* the upperside is black in costal and basal areas, and apical half posterior to vein 6 is widely dull light blue, which includes black E^2 marking in cell 2 and black tornal spot.

3) *Upperside of female forewing*

In all species except *kiana,* the female forewing always has an oblique discal orange band, which is usually bordered by discocellulars, so that it does not invade the discoidal cell in most species. But in some subspecies of *epicles,* the orange marking is much expanded to a large rounded marking occupying most of discal area of the wing, which invades the posterodistal portion of discoidal cell. In *kiana,* forewing upperside is entirely blackish without any markings as

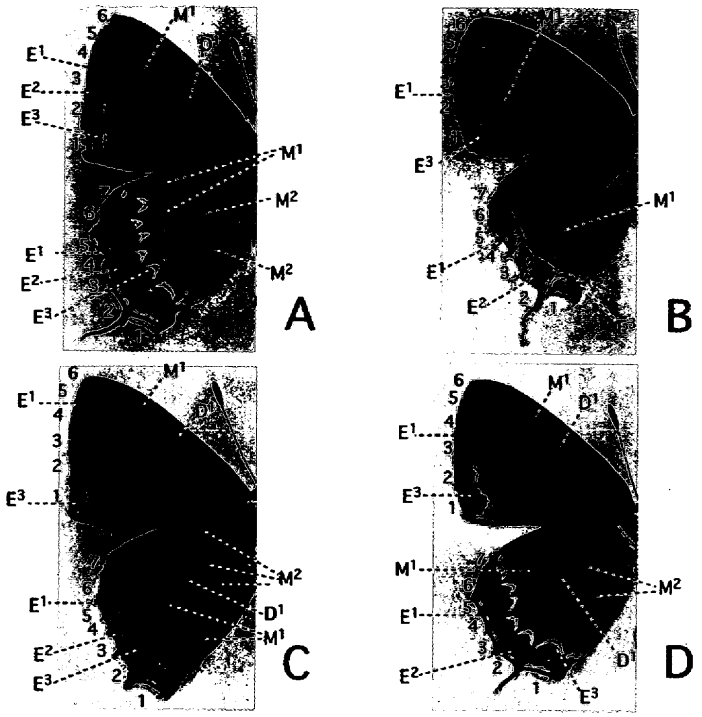

Fig. 10. Wing markings of *Heliophorus* based on the ground plan of Schwanwitsch (1949). A: *Heliophorus* (*Heliophorus*) *epicles*. B: *Heliophorus kiana*. C: *Heliophorus* (*Kulua*) *tamu*. D: *Heliophorus* (*Kulua*) *saphir*.

in the male.

4) *Upperside of female hindwing*

Female of *kiana* has similar wing pattern as in its male, but the bluish apical area is almost replaced by white, and blackish E^2 markings appears in cells 1b+c and 3. In other species, the upperside is extensively black, with orange submarginal lunules, of which the degree of development is variable by species or subspecies. In some subspecies of *epicles* and *ila,* the discal area of hindwing upperside has orange markings, which may expand to near the termen.

5) *Underside of forewing*

No fundamental sexual dimorphism is found in the markings of underside of the wings. Underside of wings is yellow to yellowish-brown in ground colour. There is a tendency for the ground colour to be slightly brighter in the *epicles* group and *kiana* than in some species of the *tamu* group, but even in the latter some species such as *brahma* has bright ground colour as in the *epicles* group. D^1 completely disappears in the *epicles* group and *kiana,* and rarely appears as a small obscure spot near the posterodistal corner of the discoidal cell in the *epicles* group. D^1 almost always appears as a distinct line extending the whole length of the discocellulars in the *tamu* group. In *saphir,* D^1 appears as in the *tamu* group, but fainter than in most species of the group.

M^1 is represented by a series of short fine lines or dots, which are completely divided by veins in the *epicles* group, but sometimes completely absent. Though M^1 in the *epicles* group rarely appears in a complete series from costa to cell 1b+c, it usually appears in cell 1b+c. In the *tamu* group, M^1 appears as a distinct, continuous streak from costa to vein 2. But it is rarely obscure posteriorly, or is represented by an undulate line curved at the veins. M^1 of the *tamu* group always disappears in cell 1b+c. In *kiana,* M^1 is represented by a series of minute, obscure dots in the posterior portion of the wings including cell 1b+c.

E^3 is represented by a series of white lines or dots usually encircled with black, and most strongly pronounced in cell 1b+c, becoming obscure and fades away towards the apex of the wing. In the *tamu* group, E^3 is represented by an obscure dark line not bordered with white anterior to vein 3. E^3 in cell 1b+c is linear in the *epicles* group and *kiana,* thick and oval in the *tamu* group, and strongly developed and almost circular in *saphir.* E^2 almost always does not appear as a distinct element. It is considered to be united with E^1, and in cell 1b+c it is represented as a black border distad of the outer white line bordering black E^3. In some species of the *epicles* group, E^2 is represented by a minute black dot partially united with E^1, as a narrow black border of the outer margin of the wing in cells 2 to 4, but in some cases the

dot-like E^2 of these cells are separated from the black outer margin of E^1 by a few white scales, which seem to be a reduced condition of a white line separating a distinct E^2 from the linear marginal E^1 in the hindwing. E^2 is not distinguishable from the black outer marginal border in other species. As stated above, E^1 is represented by the fine, black, marginal border of the termen in some species, particularly of the *epicles* group, but it is usually faded away to be brownish and indistinct from the ground colour of the wing.

A reddish or reddish-brown submarginal band usually appears between E^3 and E^1. It is well developed in the *epicles* group and *kiana* occupying the entire space between E^3 and E^1, and extends throughout the termen. In the *tamu* group and *saphir* this reddish area is at most reduced to a faint band close to the termen, and most of the space between E^3 and E^1 is filled with ground colour.

6) *Underside of hindwing*

M^2 is almost always present in cell 1b+c, discoidal cell, and cell 7, but is often absent in the latter cell in the *epicles* group. M^2 is represented by minute black spots, but in the *tamu* group M^2 in cell 7 is somewhat elongate. The development of D^1 is almost as in the forewing. M^1 differs among species groups. In the *epicles* group, M^1 is represented by minute spots, which are usually black in cells 1a, 6 and 7, white in cells 1b+c to 5, but occasionally all spots are white, and in other cases the spot in cell 5 is black in the center. In the *epicles* group, M^1 is rarely completely obsolete. The arrangement of M^1 spots in the *epicles* group is characteristic: M^1 in cell 6 usually shifted inwards, so that it is situated just below that in cell 7; M^1 represented by white spots in cells 1b+c and 2 are so distinctly shifted outwardly that they are almost connected with E^3 of each cell. In the *tamu* group, M^1 is represented by a rather distinct continuous dark band extending from the costa to the inner margin of the hindwing, usually obsolete in cell 1b+c, and running almost parallel to the termen of the wing. Therefore M^1 is not connected with E^3 markings in this group. M^1 band of the *tamu* group is sometimes undulate owing to curvatures at the veins. M^1 of *saphir* is fundamentally the same as that in the *tamu* group, but it is very fine, obscure and more or less discontinuous at the veins. M^1 of *kiana* is represented by a series of white lines running anteriorly from cell 1a up to cell 5. In this species, M^1 of cell 1b+c is rather close to E^3 marking, but distinctly separated from E^3 in cell 2.

E^3 is represented by a series of finely black-bordered white lunules various in size by species or intraspecific populations. The arrangement of E^3 markings differs among the species group. In the *epicles* group, E^3 is arranged in a zigzag line, distinctly shifted inwardly in cells 2, 4 and 6. In the *tamu* group and *saphir*, E^3 markings in cells 5 and 6 are shifted inwardly. In *kiana*, E^3 is a series of dark lines which are bordered inwardly by a broad white margin, and arranged in an evenly curved line almost parallel to the termen. E^2 in the *epicles* and the *tamu* groups and *saphir* is represented by a series of black spots, triangular markings or lines, which are placed close to E^1 represented by a fine black border along the termen of the hindwing. Distinct white lines intervene between E^1 and E^2 markings. E^2 is often covered with whitish scales in various degrees. In *kiana* E^2 is represented by a series of rounded black spots which are encircled with white and characteristically placed just midway between E^1 and E^3 markings, so that they are not close the termen of the wing. E^1 is a fine black border along the termen of the hindwing, and in some species of the *tamu* group it is brownish or even reddish, and in the latter case it is not distinguishable from the reddish submarginal area. The area between E^2 and E^3 is occupied by a reddish band, which is suffused with white scales close to E^2 except in cell 2 in all species, and in cell 6 in the *epicles* group. In *kiana*, the reddish area (more brownish in this species) is well defined in cells 5 to 7, but in the posterior cells the reddish area is obsolete owing to the expansion of the white border of E^2 and E^3.

Male genitalia

The socius is elongate and slender, divergent from the opposite socius apically, with a rounded tip in the *epicles* group, while in the *tamu* group and *saphir* the socii are short and broad basally, more or less convergent to each other beyond the middle, and distinctly tapered to a pointed tip when viewed from above. The socius of *kiana* is almost intermediate between the two groups; it is moderately long, in dorsal aspect more or less broad basally, then divergent from each other, with a rounded tip.

The falx is long and only slightly curved, and extends posteriorly much beyond the tip of the socius in the *epicles* group, while in the *tamu* group it is short and strongly curved dorsally like a fish hook, with its tip extending to the apex of the socius or only slightly beyond the apex.

The posterolateral process of the tegumen is developed in various degrees. This process is not formed in all species of the *epicles* group, *kiana*, and *viridipunctata* and *bakeri* of the *tamu* group. It is only slightly developed in *brahma*, represented by a short process in

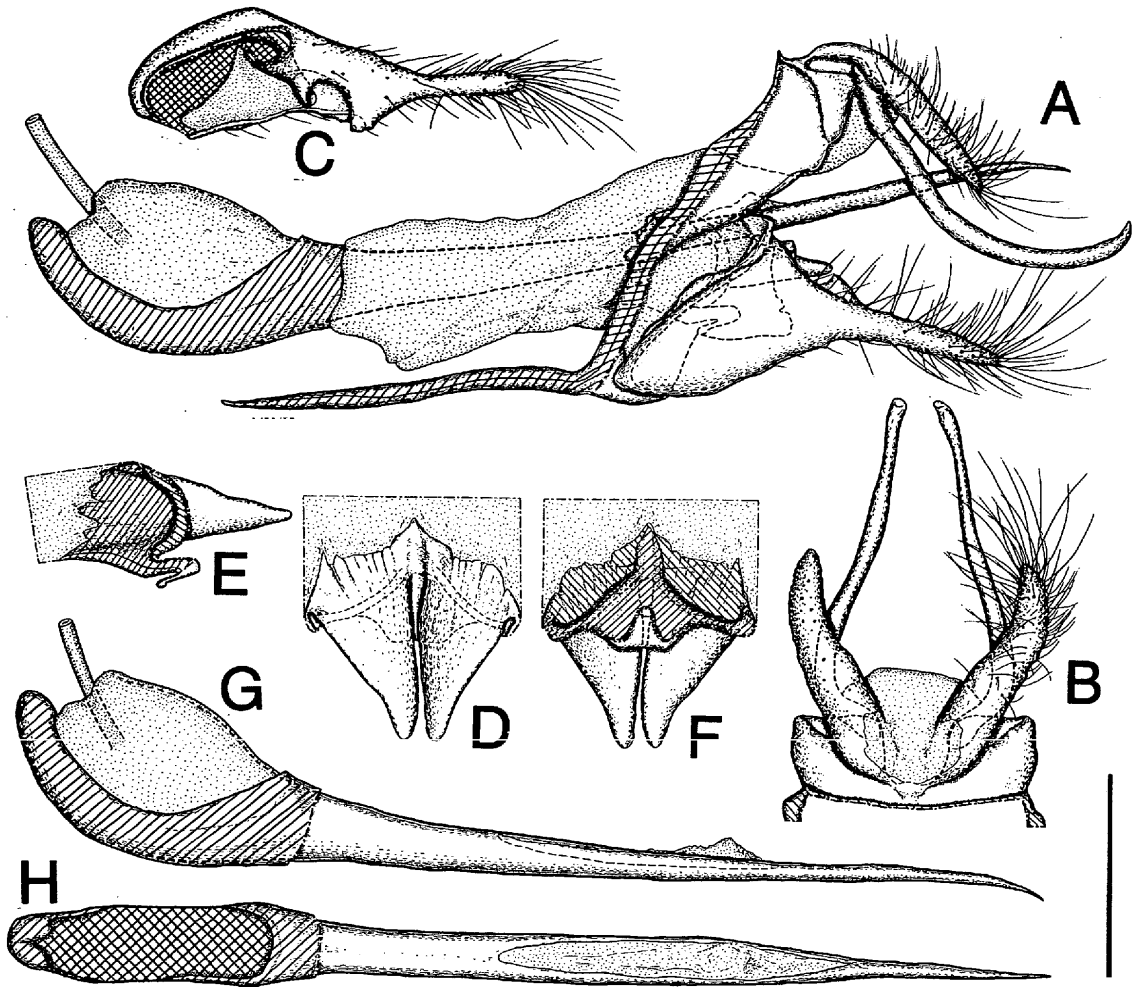

Fig. 11. Male genitalia of the *epicles* group. A–H: *Heliophorus* (*Heliophorus*) *epicles*. A: Genitalia as a whole, lateral aspect. B: Dorsum, dorsal aspect. C: Right valva, dorsal aspect. D: Juxta, dorsal aspect. E: Ditto, lateral aspect. F: Ditto, ventral aspect. G: Phallus, lateral aspect. H: Ditto, dorsal aspect. Scale bar=0.5 mm.

saphirioides. In *androcles, oda, moorei, tamu* and *saphir,* this process is enormously developed, with its tips almost extending posteriorly to the level of the apex of the socius.

The vinculum is slender throughout the genus except for *kiana,* in which it is fairly broad even ventrally.

The saccus is rather short, less than half the height of the genital ring in the *tamu* group, a little longer in *saphir* than in the *tamu* group, almost as long as the height of the ring in *kiana*. In the *epicles* group, the saccus is much longer than the height of genital ring, and in most species it is longer than the sagittal diameter of the ring.

The valva is variable in shape. In *kiana* it is rather narrow and short, only slightly tapered to the middle, then keeps the same width to its apex. In this species the inner wall of valva is simple, with an apical keel. The valva of *saphir* is more strongly elongated than in *kiana*. In the *epicles* group, it is broad basally, but much tapered to the middle, then produced posteriorly into a slender apical projection. In this group a horizontal process of various shapes projects from the base of the costa and a tuberculate process occurs at the base of the tapered apical portion on the inner wall. In the *tamu* group, the valva is large and broad. In *tamu, androcles, viridipunctata* and *brahma,* the valva is broad and oval, and furnished with dentations along the apical margin, and a transtilla-like horizontal projection extends from the base of its dorsal margin. In *oda, moorei* and *saphirioides,* the valva is still broad basally, but more or less narrowed towards a rounded apical margin, bearing a costal process projecting posterodorsally.

The juxta is moderately broad, more or less concave centrally and with a pair of horizontal lamellate processes projecting from the dorsal surface. The lamellate processes are usually short, triangular in shape,

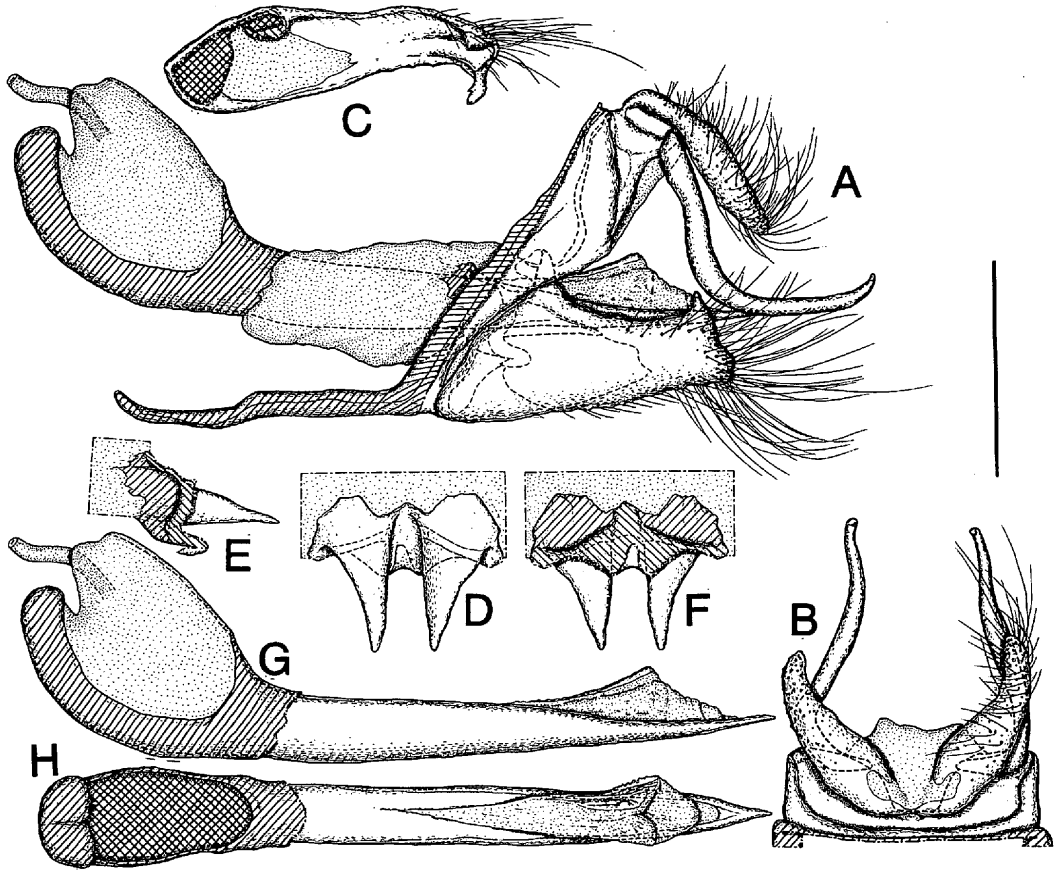

Fig. 12. Male genitalia of the *kiana* group. A–H: *Heliophorus kiana*. A: Genitalia as a whole, lateral aspect. B: Dorsum, dorsal aspect. C: Right valva, dorsal aspect. D: Juxta, dorsal aspect. E: Ditto, lateral aspect. F: Ditto, ventral aspect. G: Phallus, lateral aspect. H: Ditto, dorsal aspect. Scale bar=0.5 mm.

but in *saphir* they are enormously lengthened, so that their apices almost reach the apices of the socii. The concaved main part of the juxta is never strongly invaginated in all species.

The phallus is rather thick and about 1.5–1.6×as long as the sagittal diameter of the genital ring in the *tamu* group, *saphir* and *kiana*. In these species, the apical portion of the aedeagus is produced into a short pointed projection, the dorsal surface of suprazonal portion of the aedeagus has a wide membranous perivesical area, which usually expands near the zone. The perivesical area in *saphir* tends to be weakly sclerotized on its proximal portion. In these species, the perivesical area has a small sclerite with several denticles situated at the right side of vesical opening. The phallus is extremely lengthened in the *epicles* group. It is almost 2.5×as long as the sagittal diameter of the ring. The suprazonal portion is 2.5×as long as the subzonal portion, and is very slender. The apical projection is extremely long, almost 2/3 as long as main part of the suprazonal portion of aedeagus. The perivesical area is rather short and does not bear a sclerite.

Female genitalia

The structural modification of the female genitalia is found in the genital plate, ductus bursae, and coecum bursae. The genital plate is extremely complex and characterizes each species group. In the *epicles* group, it is a simple oval sclerite having the ostium bursae at the anterior 1/3; a small rounded or spatulate antevaginal lamellate process projects close to the ostium; the main part of the genital plate is flat and lacking special modifications, but it is desclerotized on the anterior portion in *ila*, or bears transverse wrinkles on the posterior portion in *kohimensis*. The genital plate of *kiana* is also simple, but in this species the ostium bursae opens at the tip of a short cylindrical projection arising from anterior 1/2 of the genital plate, which is flat entirely as in the *epicles* group. In the *tamu* group, the genital plate is very wide and complex; it is rather deeply invaginated on the anterior portion from which a large, broad, lamellate process projects. This lamellate process is incised medially to various degrees, so that the process is almost bifurcate in such species as *moorei*; the projected apical margins are serrate, and the median portion of the

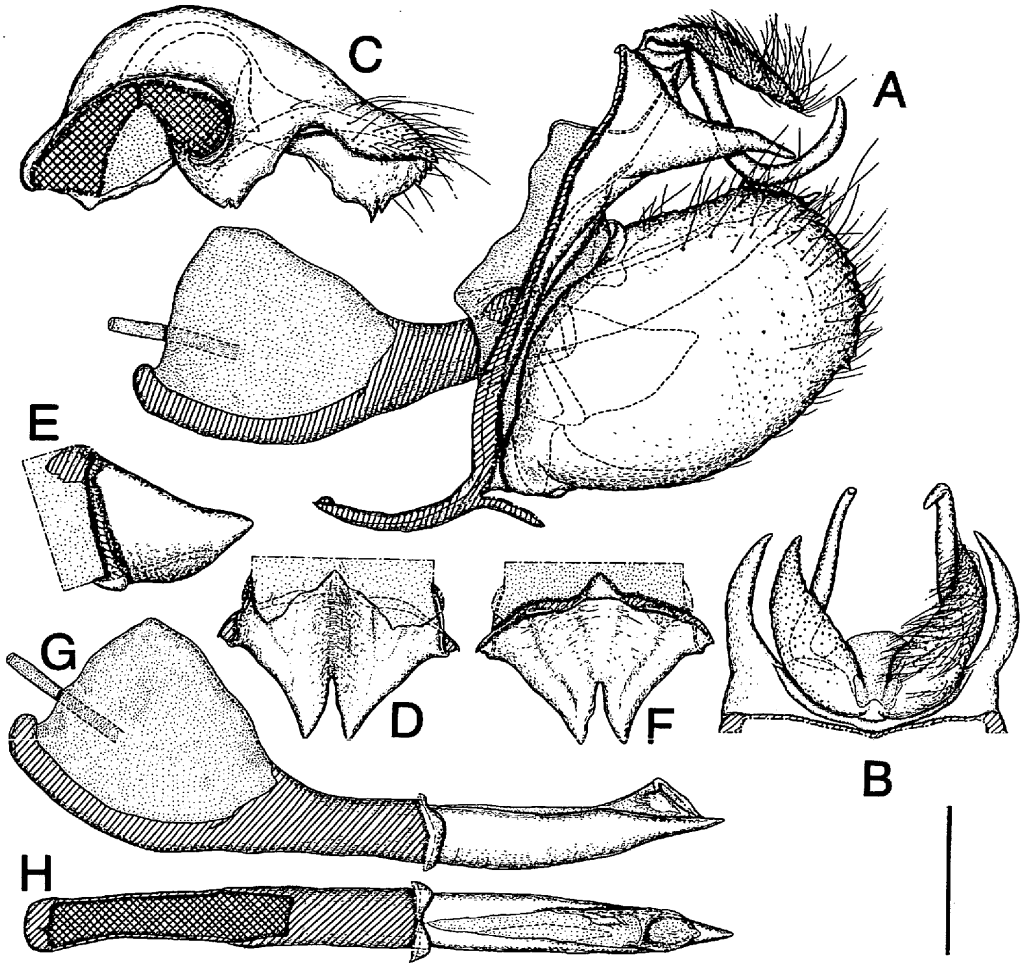

Fig. 13. Male genitalia of the *tamu* group. A–H: *Heliophorus* (*Kulua*) *tamu*. A: Genitalia as a whole, lateral aspect. B: Dorsum, dorsal aspect. C: Right valva, dorsal aspect. D: Juxta, dorsal aspect. E: Ditto, lateral aspect. F: Ditto, ventral aspect. G: Phallus, lateral aspect. H: Ditto, dorsal aspect. Scale bar=0.5 mm.

dorsal surface of the lamellate process is concaved longitudinally forming a shallow furrow. The postvaginal area of the genital plate close to the ostium is swollen medially in various degrees by species, and this protuberance is tightly pressed to the furrow of the antevaginal process. The genital plate of the *tamu* group rises like a bank along the posterior margin in various degrees by species, and the central portion of the plate is more or less desclerotized in some species. The genital plate of *saphir* is fundamentally similar to that of the *tamu* group. In this species the antevaginal lamellate process is narrower and more elongate than in the *tamu* group, and it is deeply bifurcated. The posterior marginal elevation of the genital plate is also distinctly recognizable, with a wide desclerotized area anterior to this region.

In the genus *Heliophorus* as in most lycaenine genera, the bursa copulatrix is not discriminated distinctly into the ductus bursae, cervix bursae and corpus bursae. In this paper we identify the end of the ductus bursae by the base of the coecum bursae. The ductus bursae of the *epicles* group is slender and extremely long, 1.0–2.1×as long as the 8th abdominal tergum, bearing a long, slender coecum bursae, which is 0.5–1.2×as long as the ductus bursae. The ductus seminalis arises a little posterior to the base of coecum bursae. In *kiana*, the ductus bursae is rather thick and elongated, nearly 0.9×as long as the 8th abdominal tergum; its dorsal surface is concaved. The coecum bursae is very short, and the ductus seminalis arises at the posterior 1/3 of the ductus. In *saphir*, the ductus bursae is short and broad, 0.8×as long as the 8th abdominal tergum, with a very short, protuberance-like coecum bursae. The ductus bursae of the *tamu* group is fundamentally similar to that of *saphir* but shorter, and the small protuberance-like coecum bursae is at the level of the deepest portion of the genital plate or slightly anterior to it. The ductus seminalis of the *tamu* group arises close to the ostium bursae.

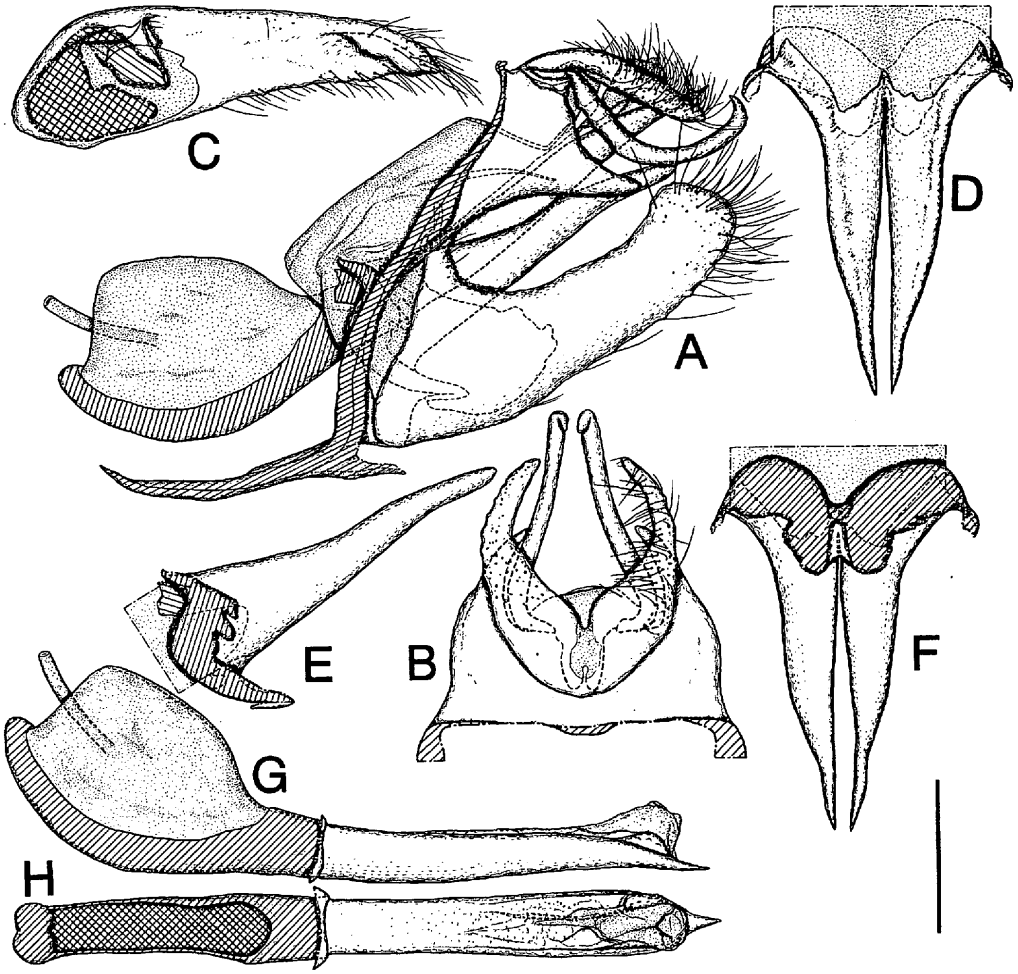

Fig. 14. Male genitalia of the *saphir* group. A–H: *Heliophorus* (*Kulua*) *saphir*. A: Genitalia as a whole, lateral aspect. B: Dorsum, dorsal aspect. C: Right valva, dorsal aspect. D: Juxta, dorsal aspect. E: Ditto, lateral aspect. F: Ditto, ventral aspect. G: Phallus, lateral aspect. H: Ditto, dorsal aspect. Scale bar=0.5 mm.

Discussion

1. *Monophyly of the genus Heliophorus*

The monophyly of the genus *Heliophorus* is not clearly demonstrated if we include *kiana* in this genus. *Heliophorus* is included in the *Heliophorus* section by Eliot (1973), Sibatani (1974), and Zhdanko (1995) by reason of the short apical claw-like projection of the male fused fore tarsi. If this character is apomorphic to the elongate claw-like structure in the *Lycaena* section, at least the *Heliophorus* section may be considered as a monophyletic group.

In the *Heliophorus* section, the genus *Melanolycaena* Sibatani, 1974 is apomorphic in the development of a single invagination of the main part of the juxta in the male genitalia, and in the slender, elongate antevaginal free process of the female genitalia. However, the latter character provides rather weak evidence in the support of the monophyly of this genus. *Iophanus* Draudt, 1920 is similar to *Melanolycaena* in wing markings, but its male genitalia is apparently more plesiomorphic than in those of *Melanolycaena*. The female genitalia of *Iophanus* was not examined. Both genera have D^2 markings on the underside of the hindwings, and in this aspect they are plesiomorphic to *Heliophorus* which lacks D^2.

Thus *Heliophorus* is separated from *Melanolycaena* and *Iophanus* by the apomorphy that D^2 marking on the underside of the hindwing is absent. The entirely yellowish ground colour with prominent submarginal orange border on the underside of wings is observed in all species of *Heliophorus*. This character may also be considered as apomorphic to the two other genera of the *Heliophorus* section. These apomorphies of wing markings are shared with *Nesa* Zhdanko, 1995, which Zhdanko included in the *Lycaena* section. The reasons for his assignment of *Nesa* to the *Lycaena* section are concidered very weak. Among the characters he mentioned, those concerning wing shape are found in

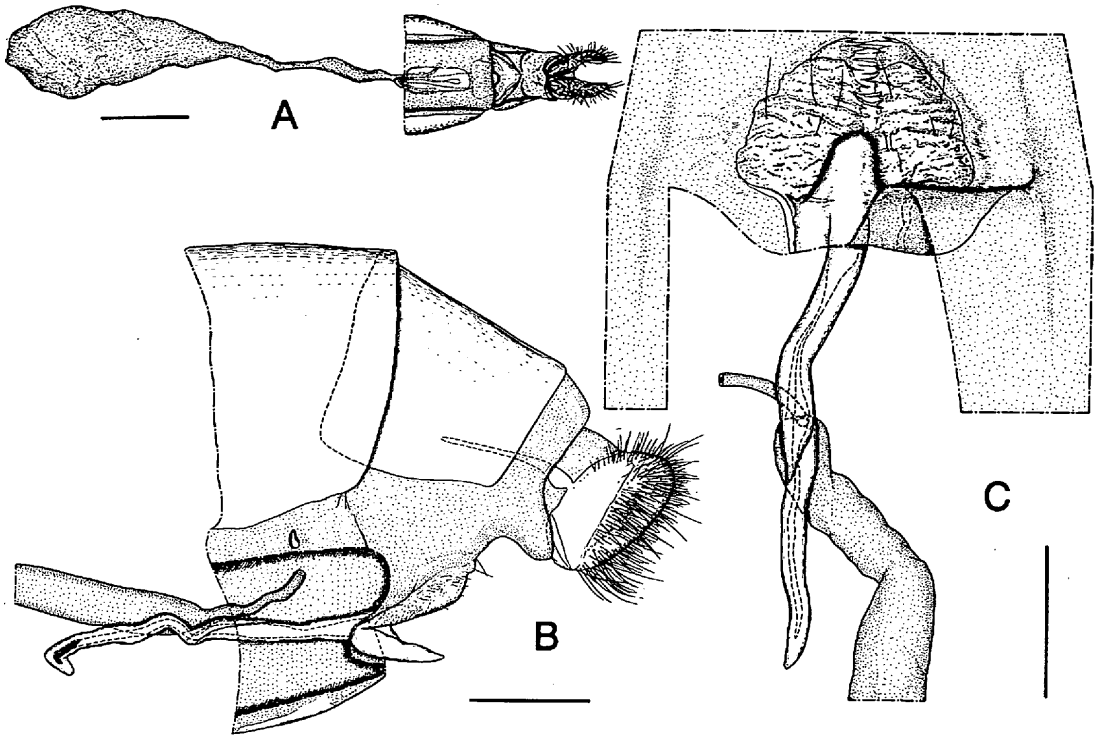

Fig. 15. Female genitalia of the *epicles* group. A–C: *Heliophorus* (*Heliophorus*) *epicles*. A: Genitalia as a whole, ventral aspect. B: Genitalia except for corpus bursae, lateral aspect. C: Genital plate, ventral aspect. Scale bars = 1.0 mm (A); 0.5 mm (B); 0.5 mm (C).

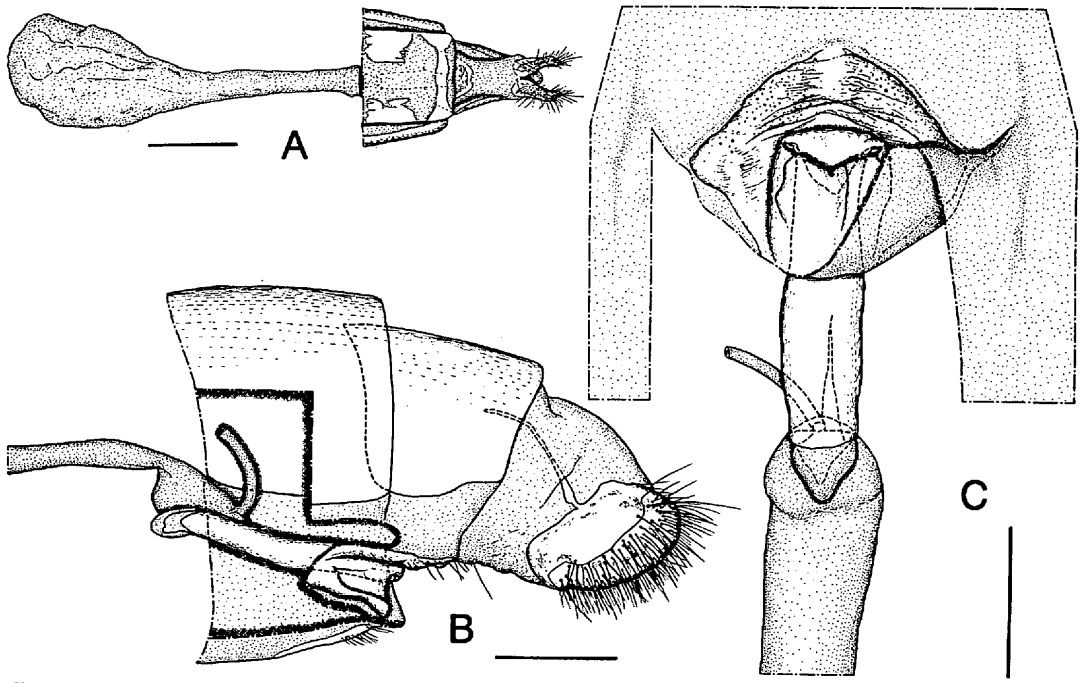

Fig. 16. Female genitalia of the *kiana* group. A–C: *Heliophorus kiana*. A: Genitalia as a whole, ventral aspect. B: Genitalia except for corpus bursae, lateral aspect. C: Genital plate, ventral aspect. Scale bars = 1.0 mm (A); 0.5 mm (B); 0.5 mm (C).

H. bakeri; the character 3 on the tint and extent of the violet marking on the upperside of the male forewing is not applicable, i.e. the same condition as *Nesa* is found on some species of *Heliophorus* including the type *epicles*; the character 4 on the orange submarginal marking on the upperside of the forewing is only symplesiomorphic among genera of the *Lycaena* section; the genitalic characters he mentioned do not

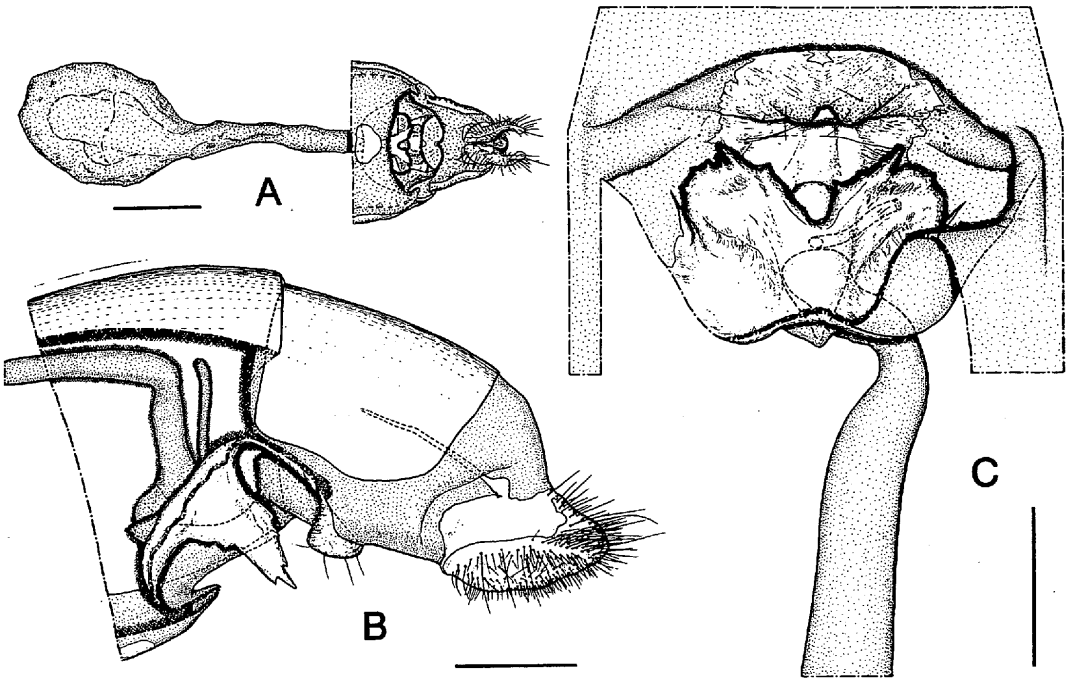

Fig. 17. Female genitalia of the *tamu* group. A–C: *Heliophorus* (*Kulua*) *brahma*. A: Genitalia as a whole, ventral aspect. B: Genitalia except for corpus bursae, lateral aspect. C: Genital plate, ventral aspect. Scale bars = 1.0 mm (A); 0.5 mm (B); 0.5 mm (C).

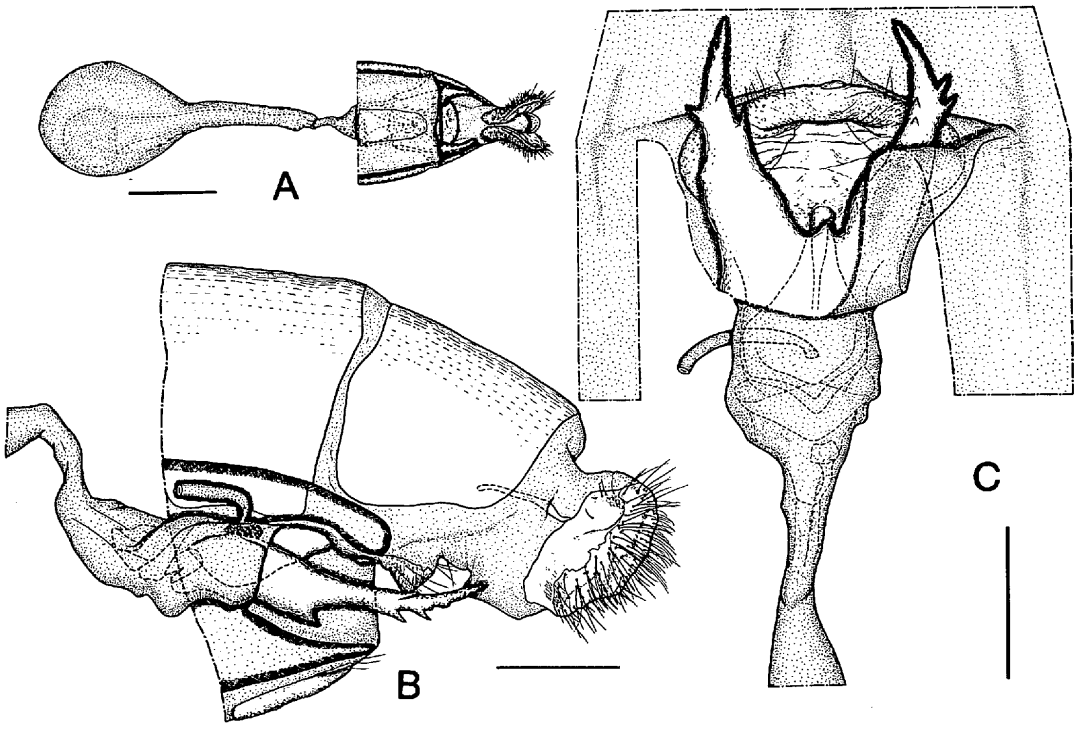

Fig. 18. Female genitalia of the *saphir* group. A–C: *Heliophorus* (*Kulua*) *saphir*. A: Genitalia as a whole, ventral aspect. B: Genitalia except for corpus bursae, lateral aspect. C: Genital plate, ventral aspect. Scale bars = 1.0 mm (A); 0.5 mm (B); 0.5 mm (C).

reliably separate *Nesa* from the *Heliophorus* section as the apparent autapomorphies of the male and female genitalia of the two sections of the Lycaeninae are not demonstrated by him. Moreover, the articulation of the 2nd and 3rd palpomeres and the apical projection of the male foretarsus of *Nesa* are very similar to those of *Heliophorus*. Therefore, we consider that *Nesa* should be included in the *Heliophorus* section.

Nesa is plesiomorphic to *Heliophorus* including *kiana* by the presence of the submarginal orange markings on the upperside of the forewing. Thus *Heliophorus* seems to be monophyletic by reason of the above-mentioned wing marking characters.

If we exclude *kiana* from *Heliophorus,* its monophyly is well supported by the following prominent autapomorphies in the wing markings. The orange discal area on the upperside of the female forewing is the most significant autapomorphy of *Heliophorus* excluding *kiana.* E^2 of the underside of the hindwing is very close to E^1 in *Heliophorus* excluding *kiana,* but this marking is situated midway between E^1 and E^3 in *kiana* and *Nesa.* The uniformly blackish uppersides of the forewings of both sexes in *kiana* are unique to this species and apparently apomorphic in the subfamily Lycaeninae, as such a condition is never found in the *Lycaena* section.

2. *Generic assignment of H. yunnani*

H. yunnani was assigned to *Heliophorus* by D'Abrera (1993). The male genitalia of this species have basic structure of the lycaenine genitalia in the structure of socius, falx, and juxta. The female of this species has a large orange discal area, which is an important autapomorphy of *Heliophorus. H. yunnani* is peculiar in the rounded wings, lacking tails on the hindwings, and much reduced wing markings on the underside of the wings. But these conditions are likely secondary specializations from the basic pattern in *Heliophorus.* The rounded wings without tails are not interpreted as plesiomorphic one found in many species and genera in the *Lycaena* section. Thus *H. yunnani* belongs to the genus *Heliophorus* as originally assigned by D'Abrera (1993).

3. *Intrageneric classification of Heliophorus*

Zhdanko (1995) divided *Heliophorus* into two subgenera, *Heliophorus* s. str. and *Kulua,* and assigning *epicles* and its allies and *kiana* to the subgenus *Heliophorus,* and *tamu* and its allies including *saphir* to *Kulua.* Among the characters used by him to separate the two subgenera, relative lengths of 2nd and 3rd palpomeres are not reliable as described in the section of morphological diversity. The submarginal orange band on the underside of the forewing and some genitalic characters mentioned by him seem to be important to separate the subgenera.

We recognize the following three major monophyletic groups in this genus. The polarity of the characters used in the following discussion was determined by comparison with most other lycaenine genera.

1. *H. kiana* group.

Autapomorphies of this group are as follows.

1) Absence of metallic discal patch on the upperside of male forewing.
2) Absence of orange discal patch on the upperside of female forewing.
3) Broad bluish or whitish area on apical portion of upperside of hindwing.
4) Long and evenly broad hindwing tail.
5) Cylindrical projection of the female genital plate with ostium bursae.

2. *H. epicles* group (subgenus *Heliophorus* of Zhdanko (1995) excluding *kiana*)

Autapomorphies of this group are as follows.

1) M^1 marking in cell 2 on underside of hindwing strongly shifted outwardly in contact with E^3 marking.
2) E^3 markings on underside of hindwing arranged in a zigzag line.
3) Male phallus extremely lengthened, with much elongate apical projection.
4) Male phallus without sclerite on perivesical area.
5) Male saccus extremely long, more than sagittal diameter of the genital ring.
6) Male socius rather evenly slender in both dorsal and lateral aspect, and ending in blunt tip.
7) Male falx extremely lengthened, and very weakly curved.
8) Female ductus bursae much elongated.
9) Female coecum bursae long and slender.

3. Subgenus *Kulua*

Autapomorphies of this group are as follows.

1) M^1 on underside of wings arranged in a continuous band.
2) M^1 on underside of forewing absent in cell 1b +c.
3) E^3 on underside of hindwing shifted inwardly in cells 4 and 5.
4) Female genital plate with large lamellate antevaginal process more or less bifurcate.
5) Female genital plate with bank-like swelling along posterior margin.
6) Female genital plate with rounded swelling just behind ostium bursae
7) Female ductus bursae short.

Resemblances between the *epicles* group and *kiana* are found in the reddish submarginal band on the underside of the forewings and the simple genital plate with flat posterior portion. These character states are

apparently plesiomorphic in *Heliophorus*, and do not represent evidence to unite them into a monophyletic group.

In the subgenus *Kulua*, *saphir* differs from other members in the following characters: 1) hindwing not elongated, its inner margin almost as long as costa; 2) hindwing tail long and slender as in the *epicles* group; 3) M^1 on the underside of wings represented by a series of fine lines; 4) male genital valva narrow rather than oval as in other species; 5) basal portion of antevaginal process narrow. These character states are apparently plesiomorphic to those found in other species of *Kulua*. On the other hand, the juxta of *saphir* has a pair of extraordinarily elongate processes, and E^3 marking on the underside of hindwing is extremely enlarged, which are apparently autapomorphies of this species. Thus the subgenus *Kulua* consists of two monophyletic groups, *saphir* and a group including other species. The latter has the following autapomorphies: 1) hindwing inner margin distinctly longer than costa, so that the wing is produced to the tornus; 2) hindwing tail short and broad; 3) M^1 on underside of wings arranged in a conspicuous continuous band; 4) female genital plate very wide anteriorly with wide lamellate flange of antevaginal process; 5) female ductus bursae extremely short; 6) male genital valva tending to be oval or spherical.

The relationship among *kiana*, the *epicles* group and *Kulua* is not clear. The outward shift of E^2 on the underside of the hindwing is considered to be apomorphic, so that the latter two groups probably compose a monophyletic group.

4. *Systematic position and evolution of H. yunnani*

As stated above, *Heliophorus* consists of three monophyletic groups, namely the *kiana* group, *epicles* group and *Kulua*, with the latter further divided into the *saphir* subgroup and the *tamu* subgroup. *H. yunnani* does not share autapomorphies with the former two groups, but possesses autapomorphies 3, 4 and 6 of *Kulua*. Therefore *yunnani* belongs to the *Kulua*-clade. However, this species does not have autapomorophies 1, 2, 5 and 7 of *Kulua*. As the underside marking of this species is much specialized and reduced, characters concerning autapomorphies 1 and 2 are obsolete in this species. As the genital plate of *yunnani* is simple along its posterior margin, this species is considered to have differentiated from an early evolutionary stage of *Kulua* before its sister species (ancestor of other species) specialized in the swelling of the female genital plate. On the other hand, *H. yunnani* is specialized in the following autapomorphies, most of which are unique in *Heliophorus*: 1) wings rounded with evenly curved termens; 2) hindwing lacking tail; 3) M^1 on underside of both wings absent; 4) undersides of both wings lacking the black markings of E^1, E^2 and E^3; 5) the space between E^1 and E^3 extremely widened; 6) ground colour of discal area on underside of forewing orange in both sexes; 7) male genital valva with slightly swollen subbasal area bordered by internal ridge; 8) male genital juxta with a pair of deep invaginations and a pair of long processes. Thus the subgenus *Kulua* consists of three subgroups, namely the *yunnani*, the *saphir* and the *tamu* subgroups.

H. yunnani is considered to have evolved at an early period of evolution of the *Kulua*-clade adapting to a grassland environment in the subalpine (subarctic) zone in high altitudes of NW Yunnan. This species is specialized in many morphological characters including the changes of the thecline-type wing shape of *Kulua* to the more ancestral, grassland *Lycaena*-like wing shape and the reduction of the thecline-type streaks on the undersides of wings and enormously developed male juxta.

5. *Systematics of Heliophorus*

The following is our system of the genus *Heliophorus* based on the above-mentioned characters. Species marked with an asterisk were not examined. Assignment of these species was based on the illustration of the wings and the male genitalia made by Riley (1929), Eliot (1965), D'Abrera (1993) and Chou (1994).

Genus *Heliophorus* Geyer, 1832

Subgenus *Heliophorus* Geyer, 1832

(a) *epicles*-group

epicles (Godart, [1824]), *ila* (de Nicéville, [1896]), *kohimensis* (Tytler, 1912), *indicus* (Fruhstorfer, 1908), *cantliei* Eliot, 1965*

Subgenus unnamed

(b) *kiana*-group

kiana Grose-Smith, 1889

Subgenus *Kulua* Zhdanko, 1995

(c) *tamu*-group

tamu (Kollar, [1844]), *brahma* Moore, [1858], *androcles* (Westwood, [1852]), *viridipunctata* (de Nicéville, 1890), *moorei* (Hewitson, [1865]), *saphirioides* Murayama, 1992, *oda* (Hewitson, [1865]), *bakeri* Evans, 1927*, *hybrida* (Tytler, 1912)*, *pulcher* Chou, 1994*

(d) *saphir*-group

saphir (Blanchard, 1871)

(e) *yunnani*-group
yunnani D'Abrera, 1993

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