



A revision of the *Pieris napi*-complex (Lepidoptera: Pieridae) and similar species with distribution in China

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<https://zoobank.org/CC0AB5E5-6532-4E9E-B5D0-2FD08B5FFE2C>

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Received 11 April 2022

Accepted 16 December 2022

Published 15 March 2023

Academic Editor Martin Wiemers

Citation: Ge SX, Jiang ZH, Wang JQ, Song K, Zhang C, Hu SJ (2023) A revision of the *Pieris napi*-complex (Lepidoptera: Pieridae) and similar species with distribution in China. *Arthropod Systematics & Phylogeny* 81: 257–287. <https://doi.org/10.3897/asp.81.e85191>

Abstract

The taxonomic status of the *Pieris napi*-complex and similar species which occur in China are revised. Relevant species distributed in the adjacent regions were included to clarify the status of Chinese species and were briefly revised. All those species are described and illustrated and new synonyms are established. A molecular phylogenetic analysis is also performed on the species group including similar species, to investigate the phylogenetic relationships between taxa. Species of the *Pieris napi*-complex that occur in China and adjacent regions are redefined, with four similar species excluded (*P. melaina*, *P. extensa*, *P. chumbiensis gyantsensis* and *P. melete*). A distribution map and keys of the complex including similar species are provided. The taxon *P. mihon* Yakovlev, 2006 stat. nov. is raised from subspecies to species status; *P. narina* Verity, 1908 stat. rev. is confirmed as a distinct species rather than a subspecies of *P. ochsenheimeri*; *Pieris euorientis* Verity, 1908 stat. rev. is recovered as a distinct species sister to *P. dulcinea*. Two taxa, ssp. *sauron* and ssp. *bryonides* are moved from subspecies of *P. euorientis* and *P. bryoniae*, respectively, to *P. napi*, i.e. *P. napi sauron* Yakovlev, 2004 comb. nov. and *P. napi bryonides* Sheljuzhko, 1910 comb. rev. A new synonym is proposed: *Pieris ochsenheimeri tianshansis* Tadokoro, Shinkawa & Wang, 2014, new synonym of *P. mihon* Yakovlev, 2006. A new mistaken identification is proposed: *Pieris dulcinea kneitzi* is a misidentification of *Pieris erutae kneitzi* Eitschberger, 1983 comb. rev. Five Chinese species belonging to the *Pieris napi*-complex were confirmed, namely *P. narina*, *P. mihon*, *P. latouchei*, *P. dulcinea*, and *P. erutae*. Among them, two species, *P. mihon* Yakovlev, 2006 and *Pieris narina* Verity, 1908, are newly recorded from China. The taxonomic status of *Pieris steinigeri* Eitschberger, 1983 and *Pieris bryoniae sifanica* Grum-Grshimailo, 1895 is also discussed.

Key words

Pieris napi-complex, phylogeny, systematics, distribution

1. Introduction

The family Pieridae, which includes over 1,000 species in 83 genera, is a large group of butterflies which plays an important role in evolutionary biology (Courtney 1986; Ackery et al. 1999; Braby 2005; Wahlberg et al. 2014). As the type genus of the family, *Pieris* is a cosmopolitan genus which contains some model animals and also several important pests (Agrawal and Kurashige 2003; Wang et al. 2020; Arikawa et al. 2021). However, as one of the genera with the highest species diversity in the family, many *Pieris* species are threatened to some extent, except for the well-known pests (David 2015). Due to their high diversity and ubiquitous intergenerational polymorphism, the taxonomic status and identification characteristics of many *Pieris* species have been very confusing, especially the *P. napi*-complex and related species.

The *P. napi*-complex has never been accurately defined. Leech (1892) firstly classified Chinese *Pieris* species with dark veinous patterns on their hindwings into three species based on size: the small-sized grey-veined white was identified as *P. napi*, the medium-sized as *P. melete* and the large-sized as *P. extensa*. Warren (1961) initially separated the *P. napi* and the *P. melete* groups by the form of androconia. After that, many *Pieris* taxa with similar characteristics were found and described (Sheljuzhko 1960, 1963, 1964, 1969). Due to the confusion surrounding these “grey-veined” whites, Eitschberger (1983) made a comprehensive revision based on integrated morphological characteristics of almost all the species in the world and described some new taxa, new combinations and new synonyms; most of the follow-up studies for revision or description of new taxa were based on this study. Tadokoro et al. (2013) carried out a phylogenetic analysis of some East Asian species to preliminarily define the *P. napi*-complex, which saw the exclusion of *P. melete* and *P. extensa* from the complex. However, despite these previous studies, the taxonomic status of the *P. napi*-complex and similar species is still fraught with challenges. Although some regional work has provided important materials and information for the taxonomy of the *P. napi*-complex and related taxa (Tuzov 1993; Tuzov et al. 1997), a comprehensive worldwide sample collection or even from a major biogeographic region is very difficult, due to the wide distribution of this species complex. The numerous synonyms in this group and the superficial description of many taxa have posed challenges to the phylogenetic and taxonomic research of this group (e.g., original descriptions of taxa belonging to *P. napi*). Therefore, this study aimed to make a revision of the *P. napi*-complex and related species in China and adjacent regions, through the combination of morphological and phylogenetic analyses. Most relevant species (taxa with their taxonomic status historically related to Chinese species) distributed in the regions adjacent to China were included to clarify the status of Chinese species and briefly discussed hereafter. In addition, due to the complexity of the target group in this study, the “distinct species” defined hereafter refer to

a collection of populations that show monophyly in the phylogenetic analysis based on DNA markers and can be distinguished from each other in morphology, but does not exclude the possibility of inter-species hybridization and gene introgression.

2. Materials and methods

2.1. Taxon sampling

A large number of specimens of all taxa historically considered as belonging to the *P. napi*-complex were examined and sampled from the authors' collections. Almost all the extensive material of the *P. napi*-complex in China and adjacent regions was examined, including some type photos reproduced from literature. Ninety-six specimens of species historically considered as part of the *P. napi*-complex were used in the molecular analysis, with their names, collecting information, and GenBank accession numbers provided in Table S1.

2.2. Morphological comparison

Specimens were spread for examination. Morphological terminology (Fig. 1) follows Eitschberger (1983). Spread specimens were photographed using an interchangeable lens digital camera Olympus E-M1 with a M. ZUIKO DIGITAL ED 60 mm F2.8 Macro lens. Final plates were prepared in Adobe Photoshop CC (Adobe Systems Inc., San José, CA, USA). For comparison between taxa, the lengths of forewings were measured to 0.5 mm precision.

To study the male and female genitalia, the abdomen was taken from the specimen and placed into a 1.5 ml microcentrifuge tube. Males were soaked in 10% potassium hydroxide solution at room temperature for about 24 hours. After dissection, the genitalia were then transferred to 80% glycerol for 12 h to render them transparent.

2.3. DNA Extraction, PCR Amplification and Sequencing

Butterfly genomic DNA was extracted from the legs of specimens using the D0926 Insect DNA Isolation Kit (Omega Bio-tek Inc., Norcross, GA, US), following the manufacturer's instructions. DNA extractions were checked on a 1% agarose gel, and DNA concentration and purity were determined with a JY300C electrophoresis system and a JY04S-3C gel imaging analysis system (JUNYI Electrophoresis Co., Ltd, Beijing, China).

PCR reactions were run in a 50 μ L system using the TaKaRa Ex *Taq* Kit (TaKaRa Biotechnology Co., Ltd., Dalian, China) which contained 5 μ L of 10 \times PCR buffer, 2 μ L of Template, 4 μ L of dNTP mixture (2.5 mmol/L each), 0.5 μ L of *Taq* DNA polymerase (5 U/ μ L), and 2 μ L each of forward and reverse primers (20 μ mol/L). The

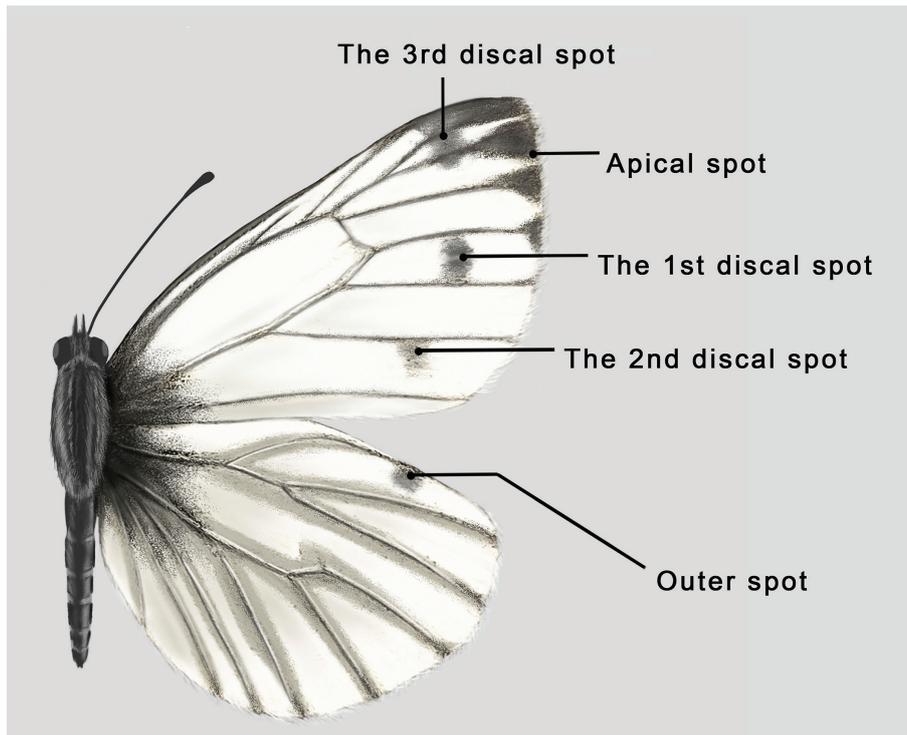


Figure 1. Fore and hind wings of *Pieris*. Morphological terminology follows Eitschberger (1983).

Table 1. Forward and reverse primers sequences in this study.

Gene	Forward primers	Reverse primers	Reference
COI	(Jerry) 5' -CAACATTTATTTGATTTTTT-GG-3'	(Pat2) 5' -TCCATTA-CATATAATCTGCCATATT-3'	Yi et al. 2017
COII	(TK-N-3785) 5' -GTTTAAGAGACCAGTACTTG-3'	(TLL) 5' -ATGGCAGATTATATGTAATGG-3'	Wang and Long 2003
ND1	5' -ATCAAAGGAGCTCGATTAGTTTC-3'	5' -CGTAAAGTCCTAGGTTAT AT TCA-GATTTCG-3'	Yi et al. 2017
ND5	(Vhs) 5' -ACTCCTGTTTCTGCTTTAGTTC-3'	(SPR2) 5' -CCATAAGTARATAAAATWGGYATA-AATC-3'	Shinkawa and Nonaka 2010
16S rDNA	(L16F2) 5' -CCGGTTTGAGCTCAGATC-3'	(L16R2) 5' -CGCCTGTTTATCAAAAACAT-3'	Aubert et al. 1999
Wingless	(LepWG1) 5' -GARTGYAARTGYCAYGGYATGTCTGG-3'	(LepWG2) 5' -ACTICGCARCACCARTGGAATGTRCA-3'	Brower and Desalle 1998

primers used are shown in Table 1. The thermal profile of the PCR run consisted of an initial denaturation step at 94°C for 3 min; 15 cycles of denaturation at 94°C for 30 s, annealing at 54°C for 30 s, and elongation at 72°C for 90 s; then a final elongation step at 72°C for 10 min. Sequences were obtained using an ABI Prism 3730XL sequencer (Applied Biosystems, California, USA). DNA sequences generated by each primer combination were used to obtain consensus sequences using Seqman v.7.1 and the DNASTAR Lasergene Core Suite software package (DNASTAR Inc., Madison, WI, USA).

2.4. Molecular phylogenetic analysis

The phylogeny was reconstructed using the Bayesian Inference (BI) method as implemented in Phylosuite (Zhang et al. 2020). We estimated the most appropriate

nucleotide substitution model by ModelFinder (Kalyaanamoorthy et al., 2017) and HKY was selected for the best-fitting model for the present phylogenetic analysis of the concatenated matrix. To further clarify their phylogenetic positions, an analysis based on the combination of 6 genes (COI, COII, ND1, ND5, 16S rDNA and Wingless) (forward and reverse primer sequences in Table 1) was carried out to compare the *P. napi*-complex and related species. The species *Aporia goutellei* (Oberthür, 1886) and *Aporia acraea* (Oberthür, 1886) were used to root the tree. All sequences were deposited in GenBank (accession numbers are ON533767–ON533857 for COI; ON521779–ON521862 for 16S rDNA; ON216320–ON216402 for COII; ON216403–ON216469 for ND1; ON216497–ON216584 for ND5 and ON216585–ON216673 for Wingless). We reconstructed the phylogeny for a dataset containing currently recognised species of the *P. napi*-complex in China and related regions

as well as some morphologically similar taxa (13 species in total, including most subspecies distributed in China and adjacent regions). BI analyses consisted of two independent runs, each with four Markov chain Monte Carlo (MCMC), which ran for 10 million generations (sampled every 1000th generation) to calculate the clade posterior probabilities (PP).

Taxa identified as monophyletic were treated as species or subspecies, while those identified as paraphyletic were further analysed using morphological characters and geographical ranges. The Kimura two-parameter (K2P) distances (Kimura 1980) between identified taxa were calculated using MEGA v.6 (Tamura et al. 2013).

3. Results

3.1. Phylogenetics of the *P. napi*-complex and similar species occurring in China and adjacent regions

The final aligned sequences for the combined dataset of ninety-six specimens included 3276 bp (776 COI, 610 COII, 386 ND1, 790 ND5, 396 16S rDNA, 318 Wingless), of which 413 sites (12.6%) were parsimony inform-

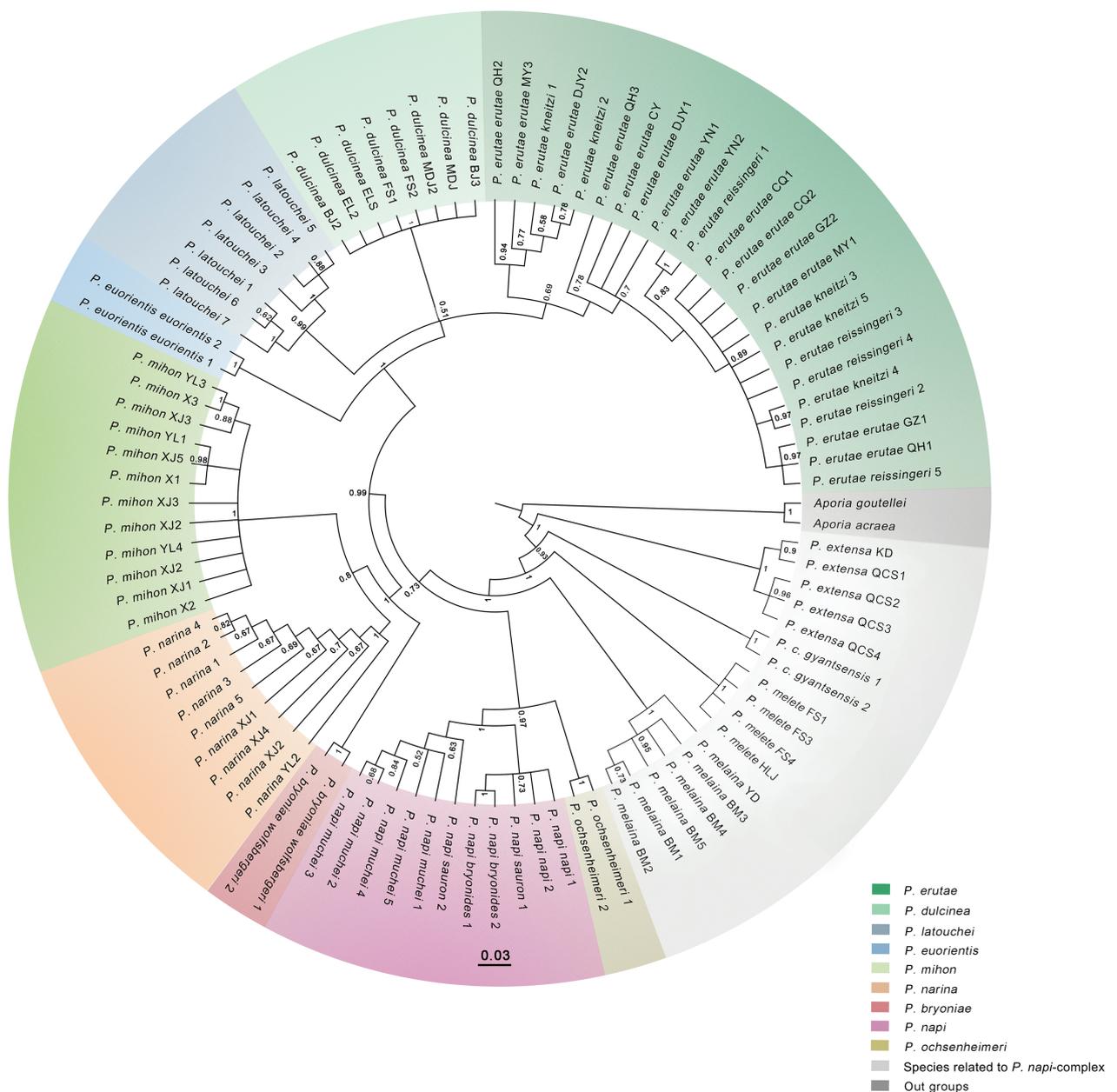


Figure 2. The Bayesian phylogenetic tree of the *Pieris napi*-complex and similar species in China and adjacent regions, with *Aporia goutellei* and *Aporia acraea* as outgroup. Coloured backgrounds delineate the species. Values at nodes indicate the posterior probability. The localities of the samples are provided in Table S1. Ladderized phylogram is shown in Figure S1.

ative. Of the maximal 776 bp of COI, 36 sites (4.6%) within the *P. napi*-complex are parsimony-informative and eight sites are singletons, as are 119 parsimony-informative sites (15.3%) and seven singleton sites within all examined *Pieris* taxa. For COII, within the *P. napi*-complex, 25 parsimony-informative sites (4.1%) and two singleton sites were found in a total of 610 bp (85 parsimony-informative sites within all *Pieris*). 24 bp (6.2%) parsimony informative within *P. napi*-complex for ND1 [58 bp (15%) within all *Pieris*]; 31 bp (3.9%) parsimony informative within *P. napi*-complex for ND5 [124 bp (15.7%) within all *Pieris*]. For nuclear Wingless, 21 (6.6%) informative variable sites were found among the *P. napi*-complex [9 bp (2.8%) parsimony informative and 12 bp (3.8%) singletons]. The ribosomal 16S rDNA harbours only 3 (0.8%) informative variable sites within the *P. napi*-complex and 15bp (3.8%) parsimony informative sites among all *Pieris* taxa.

Phylogenetic analyses of the East Asian representatives of the *Pieris napi*-complex and similar species showed that most species were well defined as monophyletic with high posterior probabilities. All the species were grouped into seven major clades (Fig. 2; Fig. S1): The first clade to branch off contained *Pieris extensa* which is thus sister to all the other species. The second clade contained *P. chumbiensis gyantsensis* which represents the *P. dubernardi*-group. The third clade contains *P. melete*. The fourth clade contains *P. melaina*. The fifth clade comprises *P. ochsenheimeri* and four *P. napi* ssp. The sixth clade contains *P. bryoniae*, *P. narina* and *P. mihon*. The seventh clade includes *P. euorientis*, *P. dulcinea*, *P. erutae* and *P. latouchei*.

Results from the Bayesian inference indicated that most taxa in the *P. napi*-complex and similar species were monophyletic, except the *P. napi* subspecies (which were mixed

at the subspecies level but formed a monophyletic clade at species level) and the *P. dulcinea* related species (with *P. dulcinea*, *P. erutae* and *P. latouchei* which turned out as a paraphyletic clade). The following taxonomic circumscriptions were derived from the results: (a) *P. melaina*, *P. extensa*, *P. chumbiensis gyantsensis* and *P. melete* have molecular lineages which are distantly separated from the *P. napi*-complex; (b) The *P. napi*-complex forms a monophyletic group that contains 9 species: *P. ochsenheimeri*, *P. napi*, *P. narina*, *P. bryoniae*, *P. mihon*, *P. euorientis*, *P. dulcinea*, *P. erutae* and *P. latouchei*; (c) ssp. *sauron* and ssp. *bryonides* are subspecies of *P. napi*, rather than being subspecies of *P. euorientis* and *P. bryoniae* respectively as previously recognised; (d) *P. mihon* is a distinct species, rather than being a subspecies of *P. euorientis*; (e) all *P. narina* cluster in a lineage which is distantly separated from *P. ochsenheimeri*, which indicates it as a distinct species; (f) *P. euorientis* is recovered as a distinct species from the subspecies of *P. napi*; (g) The phylogenetic relationships among *P. euorientis*, *P. dulcinea*, *P. erutae* and *P. latouchei* are very close, especially the latter three which are rather close to one another genetically, but can be distinguished easily on morphological characteristics.

The Kimura 2-parameter (K2P) distances (in percentage) between taxa (Fig. 3) ranged from 0.49% to 8.02%, with that between *P. euorientis* and *P. dulcinea* being the smallest, while the largest was between *P. melete* and *P. extensa*. Species belonging to the *P. napi*-complex had a K2P distance within 2%. It is noteworthy that the K2P distance between each of *P. dulcinea*, *P. erutae*, *P. euorientis* and *P. latouchei* was around 0.6%. Most K2P distances between identified species were greater than 1%.

Morphological examination, detailed in the revision section below, supported the species level phylogenetic analysis.

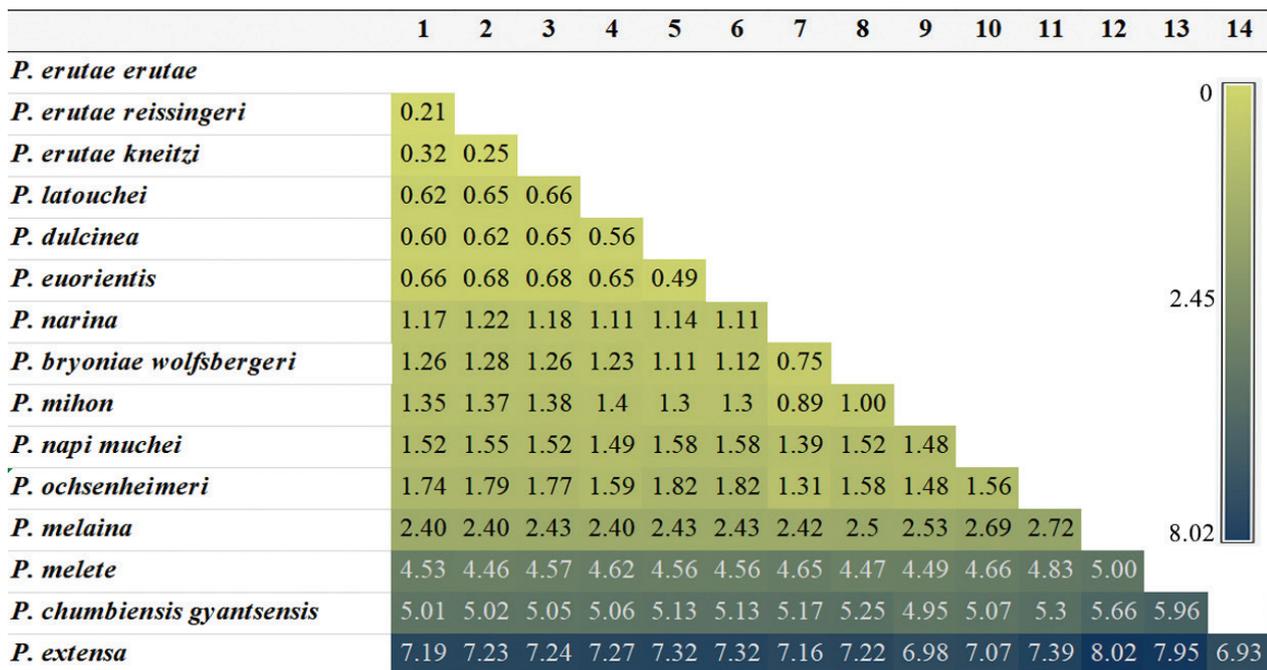


Figure 3. The Kimura 2-parameter (K2P) distances (in percentage) Matrix between taxa.

3.2. Key to males of the *P. napi*-complex and similar species in China and adjacent regions

- 1 Forewing with a distinct short black band at the end of the discocell on the upperside; the 1st discal spot distinct, oval-shaped; underside of hindwing always with well-marked black smudges in postdiscal area between the black stripes on veins (Fig. 13G). (High land: Shaanxi, Gansu, Qinghai, Tibet)..... **The *Pieris dubernardi*-group**
- 1' Forewing without a dark band or spot at the end of the discocell; the 1st discal spot variable, distinct to faintly developed; forewing without black band in postdiscal area; hindwing without dark smudges between veins on the underside2
- 2 Forewing with apical spot sickle-shaped; the 1st discal spot divided in the middle part; vein M₃ and Rs strongly blackish powdered, the outer spot distinct and merging with vein Rs on the upperside. Hindwing with humeral angle bright yellowish on the underside, distinctly contrasting to other part (Fig. 13E) (S. and S. W. China)..... ***Pieris extensa***
- 2' Forewing with apical spot variable; the 1st discal spot integrated; vein Rs without blackish dust or with all veins on the hindwing evenly dusted; the outer spot not merging with vein Rs on the upperside. Hindwing with color of humeral angle variable on the underside, mostly not distinctly contrasting to other part3
- 3 Medium to large size; hindwings without black stripes along veins on both sides or nearly so4
- 3' Medium to small size; hindwings with dark stripes along veins (at least distinctly developed on the underside)...8
- 4 Hindwing distinctly yellowish on the underside, with dark stripes along veins completely absent; Forewing with the 3rd discal spot present on the upperside (Fig. 11K) (Tian-Shan, Ghissar, Darvaz, Alai, Dzhungarsky Alatau).... ***Pieris napi muchei*** Summer form
- 4' Hindwing whitish on the underside, with dark stripes along veins completely absent or rather faintly developed; Forewing with the 3rd discal spot absent5
- 5 Forewing with basal half of discocell on the underside clearly whitish; the 2nd discal spot mostly absent on the upperside, the 1st discal spot variable.....6
- 5' Forewing with basal half of discocell on the underside dark powdered; the 2nd discal spot more or less developed on the upperside, the 1st discal spot large.....7
- 6 Forewing with apical spot and the 1st discal spot blackish and large; hindwing sometimes with darkish powder along vein tips on the outer margin (Fig. 10N) (C. China, S. C. China)..... ***Pieris erutae*** Autumn form
- 6' Forewing with apical spot and the 1st discal spot greyish and small, more or less faintly developed; hindwing without darkish powder along vein tips (Fig. 11U) (Altai and Sayan Mts, Siberia and Transbaikalia)..... ***Pieris euorientis*** Light form
- 7 Tegumen broad on its basal part and narrower in the apical half (Fig. 13K) (N. E. China, Korea, Japan, Far East Russia)..... ***Pieris melete*** Summer form
- 7' Tegumen relatively slender, with its median part slightly concave (Fig. 10C) (E. China, S. E. China)..... ***Pieris latouchei*** Autumn form
- 8 Forewing with discocell on the underside more or less dark powdered; hindwing with dark stripes narrower developed along veins on the underside9
- 8' Forewing with discocell on the underside almost clerally whitish; hindwing with dark stripes along veins variable10
- 9 Forewing with more intensively grey suffusion on the underside of discocell (almost reaching 1/2 length of discocell), all discal spots on the upperside absent or only the 1st discal spot faintly developed (Fig. 13I) (N. E. China, Korea, Japan, N. E. Russia)..... ***Pieris melete*** Spring form
- 9' Forewing with grey suffusion on the underside of discocell moderately developed (not reaching 1/2 length of discocell), the 1st discal spot rather distinctly developed on the upperside (Fig. 10G, H, L) (C. China, S. C. China).... ***Pieris erutae*** Summer form
- 10 Apical spot strongly developed, blackish, completely merging as sickle shaped with its inner margin smooth; the 1st discal spot distinct and almost reaching the apical spot (Fig. 13A, C) (S. E. Tibe, Nepal, N. E. India)..... ***Pieris melaina***
- 10' Apical spot variable, not completely merging; the 1st discal spot absent or far from the apical spot.....11
- 11 The 1st discal spot distinct and large with a trend to connect the 2nd discal spot; the 2nd discal spot faintly developed on the upperside; apical spot scattered (Fig. 9L) (Far East of Russia, Mongolia, N. E. China.)..... ***Pieris dulcinea*** Summer form
- 11' The 1st discal spot relatively small; the 2nd discal spot mostly absent on the upperside; apical spot variable12
- 12 Small and delicate, outer margin of wings (at least hindwings) blackish13
- 12' Mostly medium size, outer margin of both wings whitish.....15
- 13 Forewing with the 3rd discal spot present (Fig. 11C, D) (East Kazakhstan) ***Pieris napi sauron***
- 13' Forewing with the 3rd discal spot absent.14
- 14 Forewing with apical spot more developed, blackish, triangular extending along veins to outer margin and sometimes partly merging apically; the 1st discal spot and outer spot distinctly developed; outer marginal border of

- hindwings blackish, triangularly extending along veins (Fig. 11A) (Ghissar, Alai, western Tian-Shan).....*Pieris ochsenheimeri*
- 14' Forewing with apical spot relatively less developed; the 1st discal spot and outer spot rather faintly developed to absent; outer marginal border of hindwings blackish, sometimes linearly extending along veins (Fig. 9A) (N. and Inner Tian Shan, Dzhungarsky Alatau).....*Pieris narina*
- 15 Size relatively large; forewing with the apical spot more or less integrated as sub-triangular to sub-quadrilateral shaped and mostly not reaching vein CuA₁16
- 15' Mostly small in size; forewing with the apical spot scattered along veins, sometimes reaching vein CuA₁.....18
- 16 Hindwing distinctly bright yellow on the underside; Forewing with the 1st discal spot distinctly developed (Fig. 10B) (E. China, S. E. China).....*Pieris latouchei* Summer form
- 16' Hindwing pale yellow on the underside; Forewing with the 1st discal spot absent or rather faintly developed17
- 17 Tegumen broad, basal margin of the uncus slightly narrower than tegumen, with its apical half relatively steeply digitation (Fig. 5M–O) (C. China, S. C. China).....*Pieris erutae* Spring form
- 17' Tegumen relatively slender, with its median part more or less concave, uncus with its apical obtusely digitation (Fig. 5K) (E. China, S. E. China).....*Pieris latouchei* Spring form
- 18 Forewing with the 3rd discal spot present.....19
- 18' Forewing with the 3rd discal spot absent.....20
- 19 Tegumen with its terminal part moderately sclerotised as almost lobe-shaped convex (Fig. 5E) (N. Tian-Shan, Dzhungarsky Alatau, the Alai and Sayan).....*Pieris napi bryonides*
- 19' Terminal part of tegumen without lobe-shaped convex (Fig. 5F) (Tian-Shan, Ghissar, Darvaz, Alai, Dzhungarsky Alatau).....*Pieris napi muchei* Spring form
- 20 Hindwing almost whitish on the underside (Fig. 9D, F, H) (Bayan-Ulegei aimak, Tanguura Mountains, Xinjiang).....*Pieris mihon*
- 20' Hindwing with its underside pale yellowish or yellowish21
- 21 Forewing with the 1st discal spot relatively less developed, sometimes absent; tegumen with distinct concave near its median part, distal margin of tegumen moderately sclerotised as pairs sub-lobe shaped convex (Fig. 9J; Fig. 5L) (Far East of Russia, Mongolia, N. E. China.)*Pieris dulcinea* Spring form
- 21' Forewing with the 1st discal spot relatively more developed; tegumen without distinct concave (Fig. 11S; Fig. 5J) (Altai and Sayan Mts, Siberia and Transbaikalia).....*Pieris euorientis* Dark form

3.3. Key to females of the *P. napi*-complex and similar species in China and adjacent regions

- 1 Forewing with a distinct short black band at the end of the discocell on the upperside; the 1st discal spot distinct, oval-shaped and extended as black band in the postdiscal area; underside of hindwing always with well-marked black smudges in postdiscal area between the black stripes on veins (Fig. 13H) (High land: Shaanxi, Gansu, Qinghai, Tibet) **The *Pieris dubernardi*-group**
- 1' Forewing without a dark band or spot at the end of the discocell; forewing without black band in postdiscal area; hindwing without dark smudges between veins on the underside2
- 2 Hindwing with dark stripes along veins completely absent on the underside3
- 2' Hindwing with dark stripes along veins more or less developed on the underside4
- 3 Large size; both wings whitish with black stripes along veins absent on the underside while more or less developed on the upperside (Fig. 13L) (N. E. China, Korea, Japan, N. E. Russia)*Pieris melete* Summer form
- 3' Medium size; hindwings yellowish on the underside; dark stripes along veins completely absent on the upperside (Fig. 11L) (Tian-Shan, Ghissar, Darvaz, Alai, Dzhungarsky Alatau)*Pieris napi muchei* Summer form
- 4 Vein M₃ and vein Rs strongly blackish powdered; the outer spot distinct merging with vein Rs on the upperside, with dark area extends to the margin (Fig. 13F) (S. and S. W. China)*Pieris extensa*
- 4' Vein Rs without dark powdered or all veins on the hindwing evenly dusted; the outer spot separated from vein Rs on the upperside5
- 5 Small size; forewing with apical spot rather weakly developed, completely dividend along veins without any confusion.....6
- 5' Medium to large size; forewing with apical spot more or less integrated, distinctly contrasting to dark powdered along veins.....8
- 6 Wings almost completely whitish with all veins evenly dusted; apical spot rather faintly developed or almost absent; the 1st and 2nd discal spot relatively more developed (Fig. 9E, G, I) (Bayan-Ulegei aimak, Tanguura Mountains, Xinjiang).....*Pieris mihon*
- 6' Hindwing with its underside more or less yellowish; darkish stripes along veins at least broadened on the apex (apical spot more or less developed).....7

- 7 Forewing with the 3rd discal spot moderately developed (Fig. 11T, V) (Altai and Sayan Mts, Siberia and Transbaikalia).....*Pieris euorientis*
- 7' Forewing with the 3rd discal spot absent (Fig. 9K) (Far East of Russia, Mongolia, N. E. China.).....*Pieris dulcinea* Spring form
- 8 Small and delicate; hindwing with its outer margin blackish9
- 8' Mostly medium size; outer margin of hindwing whitish11
- 9 Wings with brownish suffusion on the upperside extremely strong developed; dark suffusion almost filling the discocell of forewings (Fig. 11E) (East Kazakhstan).....*Pieris napi sauron*
- 9' Wings with dark suffusion on the upperside strongly developed; discocell of forewing at least with its apical 1/3 clear10
- 10 Apical half of discocell on the upperside of forewings clearly whitish; hindwing with its underside whitish or yellowish (Fig. 11B) (Ghissar, Alai, western Tian-Shan)*Pieris ochsenheimeri*
- 10' Apical 1/3 of discocell on the upperside of forewing clearly whitish; hindwing with its underside yellowish (Fig. 9B, C) (N. and Inner Tian Shan, Dzhungarsky Alatau)*Pieris narina*
- 11 Apical spot rather strongly developed, blackish, completely merging as sickle shaped, combine with the 1st discal spot (Fig. 13B, D) (S. E. Tibe, Nepal, N. E. India).....*Pieris melaina*
- 11' Apical spot relatively less developed, distinctly separated from the 1st discal spot12
- 12 Forewing with the 3rd discal spot distinctly present (Fig. 11H) (N. Tian-Shan, Dzhungarsky Alatau, the Alai and Sayan).....*Pieris napi bryonides*
- 12' Forewing with the 3rd discal spot absent13
- 13 Size relatively large; forewing with the apical spot more integrated as sub-triangular to sub-quadrilateral shaped..14
- 13' Medium sized; forewing with the apical spot small, only combine between vein R₂₊₃ and vein R₅ (Fig. 13I) (N. E. China, Korea, Japan, N. E. Russia).....*Pieris melete* Spring form
- 14 Both wings clear and whitish, dark powdered along veins rather faintly developed on the underside but moderately developed apically at vein tips on the upperside (Fig. 9M) (Far East of Russia, N. E. China.)*Pieris dulcinea* Summer form
- 14' Both wings more or less brownish or yellowish, dark powdered along veins at least evenly developed on the underside15
- 15 Hindwing distinctly bright yellow on the underside; summer and autumn forms sometimes with slight lilac tone on the upperside (Fig. 10D, E) (E. China, S. E. China).....*Pieris latouchei*
- 15' Hindwing relatively pale yellowish on the underside; summer and autumn forms without lilac tone on the upperside (Fig. 10I–K, M, O, R) (C. China, S. C. China).....*Pieris erutae*

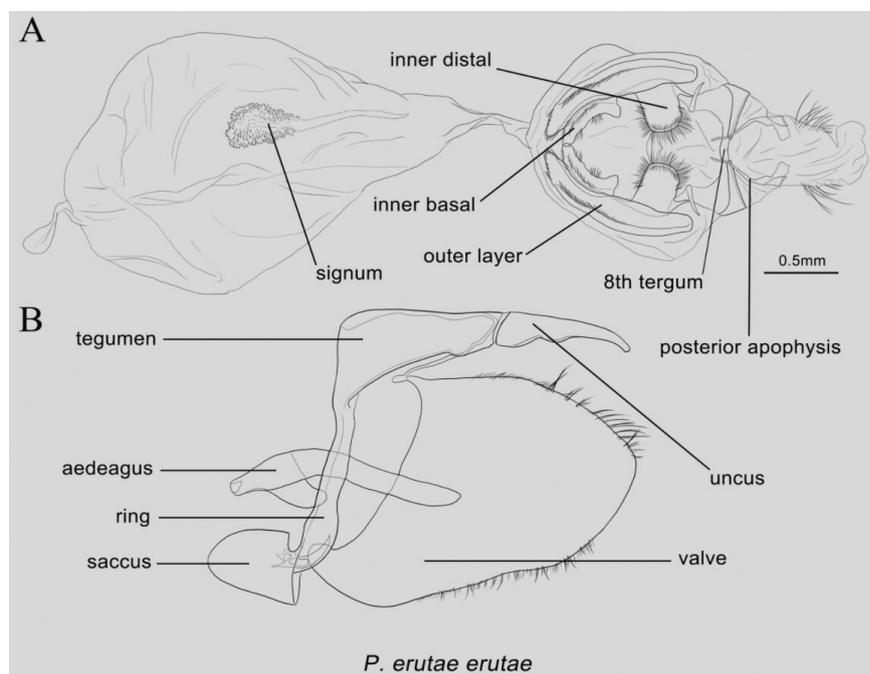


Figure 4. Nomenclature of male and female genitalia of the *Pieris* species used in this study illustrated by *P. erutae erutae* Pujade, 1888. **A** female genitalia, **B** male genitalia.

3.4. Revision of the *P. napi*-complex species in China

3.4.1. General description of male genitalia

Moderately sclerotized. Ring straight of moderate width (Fig. 4B); near perpendicular with saccus and tegumen; uncus relatively broad at base, gradually narrowed into a pointed tip distally; saccus large and broad, spindle-shaped and obtusely developed distally. Valve short,

shape conspicuously varies within taxa and individuals from sub-triangular to sub-quadrilateral. Aedeagus short and relatively robust, distinctly curved ventrally with a lobe-shaped trochanter at its ventral base; Juxta V-shaped with two arms widely apart.

3.4.2. General description of female genitalia

Papillae anales extremely short (Fig. 4A); posterior apophysis rather slender, reaching approximately the 8th

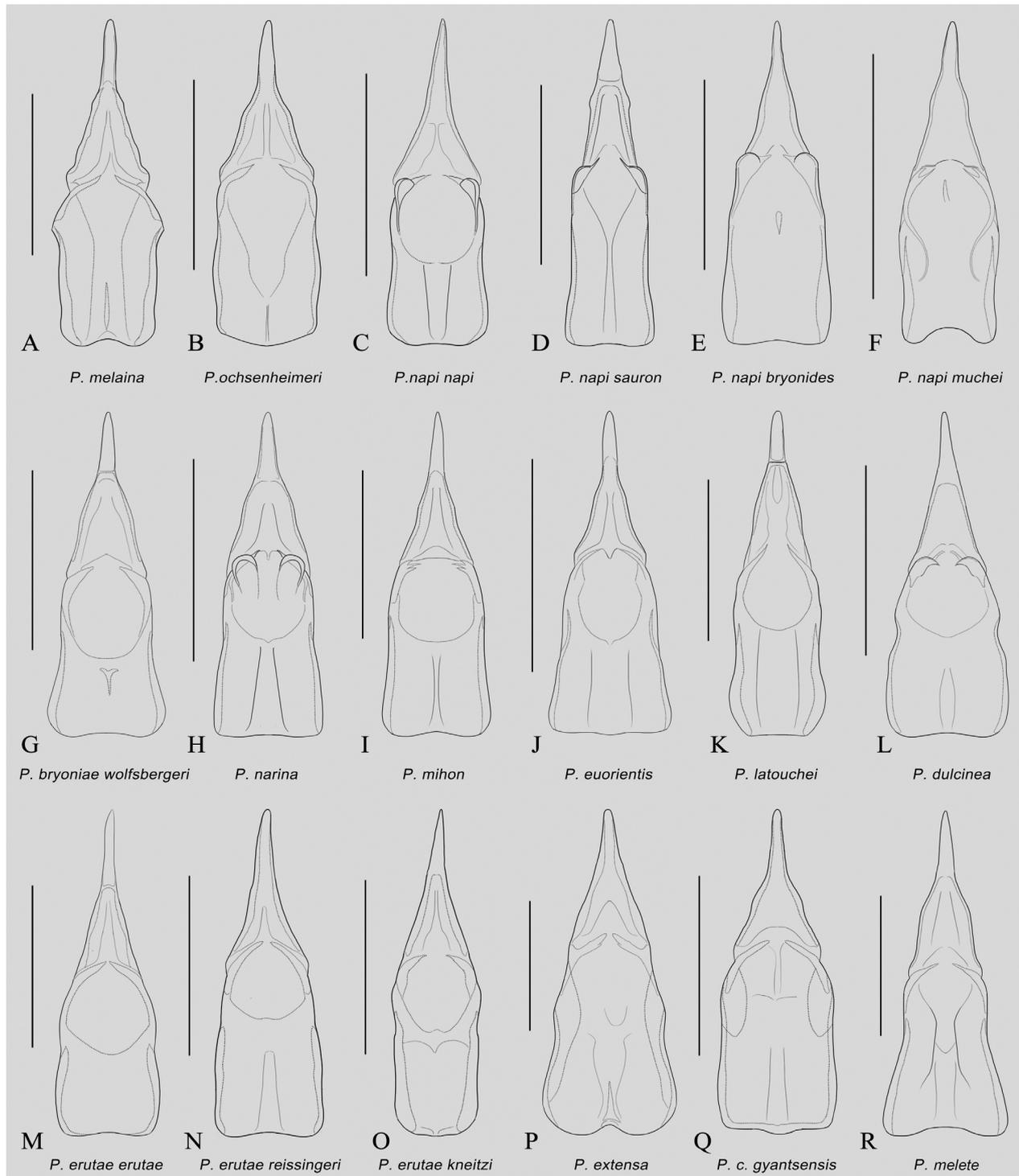


Figure 5. Tegumen and uncus of male genitalia in dorsal view. Scale bar represents 1 mm.

abdominal section; lamella postvaginalis slightly sclerotized; Ductus bursae tubular and membranous, rather slender; corpus bursae oval and always with small appendix bursae attached anteriorly, signum axisymmetric, covered with spines, cordiform-shaped in most taxa and concave at terminal margin; sterigma moderately sclerotised, densely setose with different shape between taxa.

3.4.3. Comparisons of genitalia between taxa

In general, among the *P. napi*-complex and similar species examined, genitalia structures are mostly similar not only among males but also among females. The authors found that characteristics of the tegumen and uncus in male genitalia in the dorsal view (Fig. 5) and signum of female genitalia (Fig. 6–8) can be useful for distinguishing some taxa, thus only the most important differences are reported below to avoid repetition.

Genus *Pieris* Schrank, 1801

Pieris Schrank, 1801; Fauna Boica 2(1): 152, 161; TS: *Papilio brassicae* Linnaeus, 1758.

= *Ganoris* Dalman, 1816; K. VetenskAcad. Handl. 1816(1): 61; TS: *Papilio brassicae* Linnaeus, 1758

= *Andropodum* Hübner, 1822; Syst.-alph. Verz.: 2–5, 7–9; TS: *Papilio brassicae* Linnaeus, 1758

= *Tachyptera* Berge, 1842; Schmetterlingsbuch: 19, 92–105; TS: *Papilio brassicae* Linnaeus, 1758

= *Artogeia* Verity, 1947; Le Farfalle diurn. d'Italia 3: 192, 193; TS: *Papilio napi* Linnaeus, 1758

= *Talbotia* Bernardi, 1958; Rev. franc. Ent. 25: 125; TS: *Mancipium naganum* Moore, 1884

= *Sinopieris* Huang, 1995; Bull. amat. Ent. Soc. 54(399): TS: *Sinopieris gongaensis*, Huang, 1995

Description. Small to medium size. Both wings white and sometimes with a creamy yellow hue. Apex and outer margin on the upperside of forewing blackish, with blackish 1st and 2nd discal spot always developed. Females darker than males with dark markings more developed. The third segment of labial palpus elongated.

Pieris narina Verity, 1908 stat. rev.

Pieris napi var. *bryoniae* r. *narina* Verity, 1908; Rhopalocera Palaearctica (13–14): 145, (17–20): pl. 32, f. 28–29, pl. 33, f. 2; TL: “Naryn”. (original description)

Pieris narina narina Verity, 1908; Eitschberger (1983): Herbiopoliana 1(1–2): 221–222 (infrasubspecific name validated as distinct species).

Pieris napi var. *banghaasi* Sheljuzhko, 1910; Eitschberger (1983): Herbiopoliana 1 (1–2): 221–223 (as a synonym of *P. narina*)

Pieris ochsenheimeri narina Verity, 1908; Tadokoro et al. (2014): Butterflies 65: 20–25 (as subspecies of *P. ochsenheimeri* Staudinger, 1886)

Pieris napi (Linnaeus, 1758); Wu & Hsu (2017): Butterflies of China vol. 1: 401–404, f. 15–16 [MisID]

Description. small in size. Male (Fig. 9A): both wings white on the upperside and pale yellowish on the underside. Costal margin black; apical spot blackish, triangular, extending along veins to outer margin and sometimes reached vein CuA₂. Outer margin border of forewing blackish. The 1st discal spot and outer spot variable, distinct to nearly absent on both upperside and underside. The 2nd discal spot absent or only faintly indicated on the underside and the 3rd discal spot absent or sometimes very vague on the upperside. Outer margin border of hindwings grey to blackish, sometimes triangularly extending along veins. Female (Fig. 9B, C): both wings white to pale yellowish with intensive brownish or grey suffusion on the upperside while yellowish on the underside, but clearly in the apical 1/3 of discocell on the upperside of forewing. Hindwing with dark powder strongly developed along veins.

Distribution. Kazakhstan, Kyrgyzstan, Tajikistan (Northern and Inner Tian Shan, Dzhngarsky Alatau), China (Xinjiang)

Phenology. Probably univoltine, based on a single form of adults observed in July.

Male genitalia. (Fig. 5H) terminal part of tegumen with pairs of sickle shaped convex; uncus broad with its basal part as wide as terminal part of tegumen, apical half of uncus digitation.

Female genitalia. (Fig. 6D) posterior apophysis short and slender; inner distal of sterigma bilobate lobe shaped, extend to the center; inner basal of sterigma with a distinct tooth near the basal part, acute-angled connected at the basal margin; signum relatively broad cordiform shaped, moderately tapering to the base.

Note. The species rather resembles *P. ochsenheimeri*, but can be distinguished by comparing multiple morphological characteristics (see notes in *P. ochsenheimeri*); the blackish outer marginal border on both wings and the relatively smaller size make it easily separated from other species of the *napi*-complex distributed in the same region. This taxon was formerly elevated by Eitschberger (1983) to species level while Tadokoro et al. (2014) regarded it as a subspecies of *P. ochsenheimeri*. However, this taxon has unique morphological characteristics and a previous study has shown that there is deep differentiation between *P. narina* and *P. ochsenheimeri* for the COI gene (Lukhtanov et al. 2009). Our phylogenetic results also indicated that this species is more closely related to *P. bryoniae* than to *P. napi* or *P. ochsenheimeri*, thus we confirmed it as a distinct species.

Pieris mihon Yakovlev, 2006 stat. nov.

Pieris euorientis mihon Yakovlev, 2006; Eversmannia 6: 17; TL: “W. Mongolia, Bayan-Ulegei aimak, 2100–2300 m” (original description)

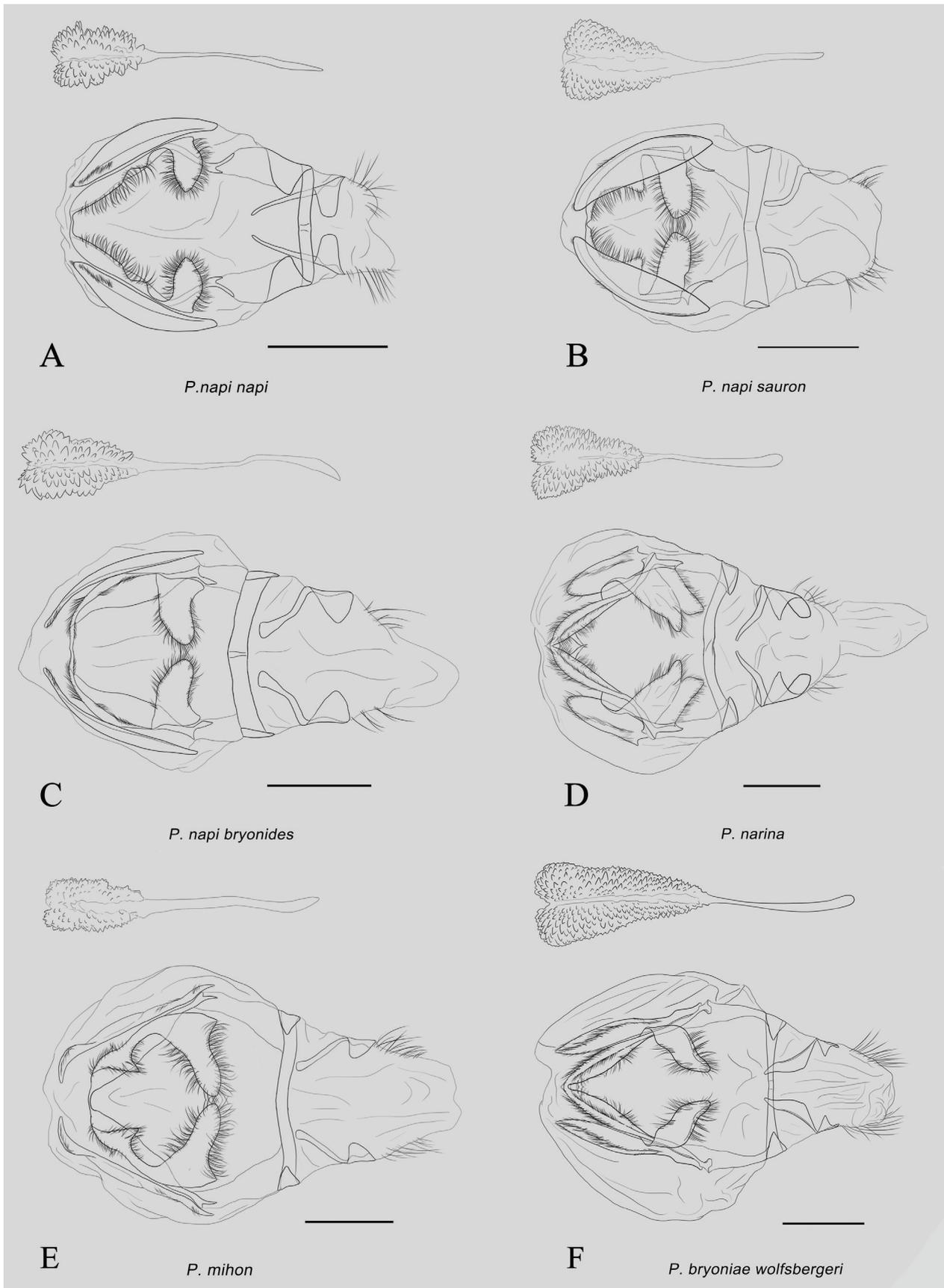


Figure 6. Female genitalia of *P. napi*-complex species. Scale bar represents 0.5 mm.

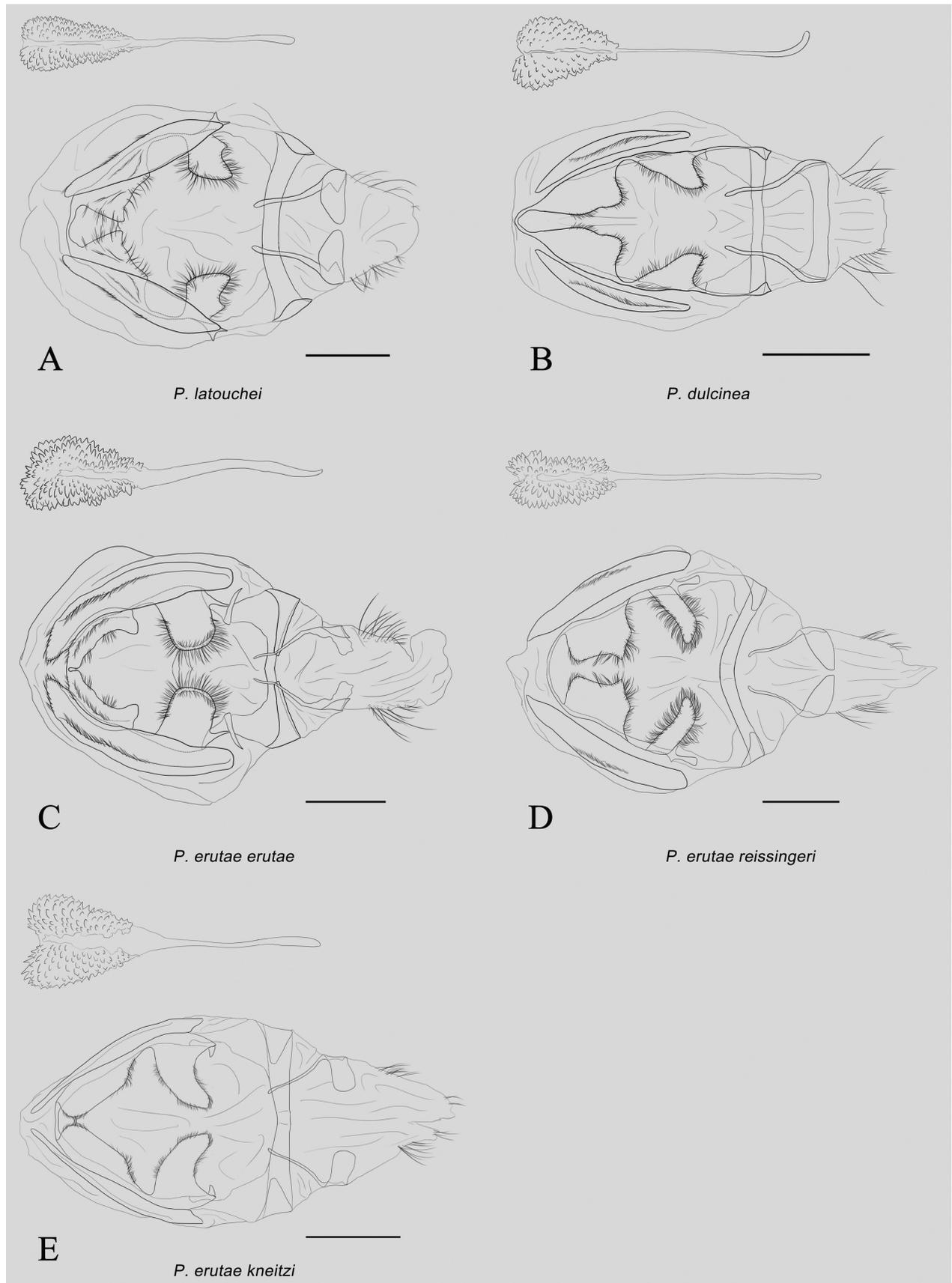


Figure 7. Female genitalia of *P. napi*-complex species. Scale bar represents 0.5 mm.

Pieris ochsenheimeri tianshansis Tadokoro, Shinkawa & Wang 2014: Butterflies 65: 20; TL: East Tianshan Mts [S. Urumuqi, Xinjiang, China] **syn. nov.**

Description. spring form: male (Fig. 9D, H): both wings whitish on both sides. Apical spot blackish, triangular, extending along veins to outer margin without merging

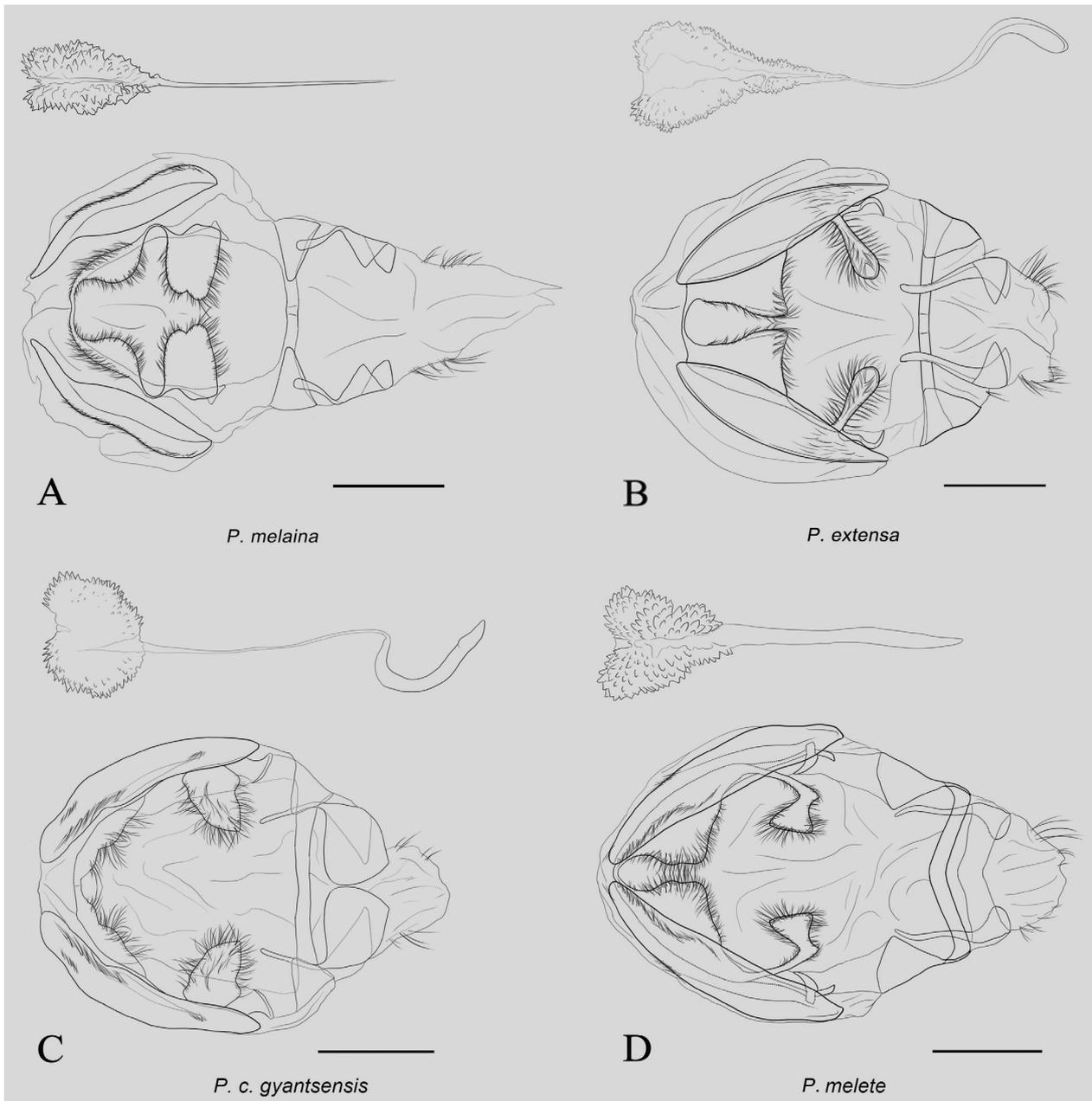


Figure 8. Habitus of species similar to *P. napi*-complex distributed in China. Scale bar represents 0.5 mm.

or suffusion. All discal spots absent or only the 1st discal spot faintly expressed, outer spot absent or faint on the upperside. Outer edge of hindwing black powdered along vein tips. Female (Fig. 9E): both wings white on the upperside and a creamy yellow hue on the underside. All veins strongly brownish powdered but narrowly developed along veins without suffusion. The 1st, 2nd, and outer spots distinct on the upperside while faintly indicated on the underside, the 3rd spot absent or rather vague on the upperside, but mostly absent on the underside. Summer form: male (Fig. 9F): resembling the first generation but the apical spot merging as an apical band running from costa to vein CuA₁. The 1st spot distinct while other spots mostly absent on the upperside; the 1st and 2nd spots present on the underside, while others absent. Female (Fig. 9G): resembling the first generation while veins less brownish powdered. All spots on the upperside rather

strongly expressed, while the 3rd spot and outer spot absent on the underside.

Distribution. West Mongolia (Bayan-Ulegei aimak), South Russia (Tanguura Mountains), West China (Xinjiang)

Phenology. Bivoltine from May to August

Male genitalia. (Fig. 5I) terminal part of tegumen without distinct convex; basal part of uncus slightly narrowed as terminal part of tegumen; uncus with moderately convex at its median part, apical half of uncus digitation.

Female genitalia. (Fig. 6E) posterior apophysis short and relatively robust; inner distal of sterigma lobe shaped, almost contact in the center; inner basal of sterigma with

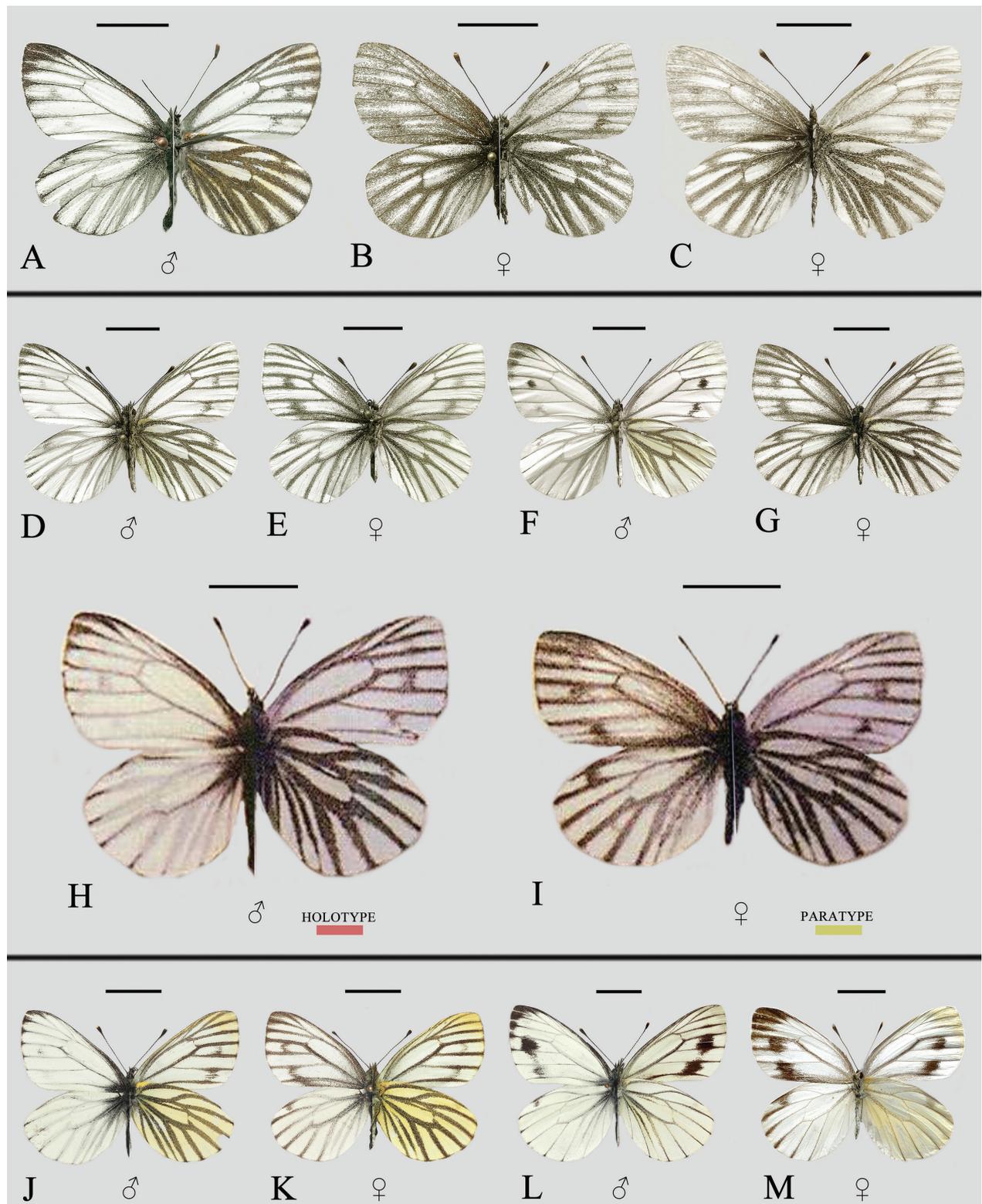


Figure 9. Habitus of *P. napi*-complex species occurring in China. Composite pictures on the left show the upperside, on the right show the underside. **A–C** *Pieris narina* stat. rev. Verity, 1908. **D–I** *Pieris mihon* Yakovlev, 2006 stat. nov. **J–M** *Pieris dulcinea dulcinea* (Butler, 1882). Scale bar represents 10 mm. (L, M reference Yakovlev, 2006).

steeply convex near the median part, smoothly connected at the basal margin; signum relatively short and slender, spindle shaped.

Note. We noticed that specimens of this taxon previously recognized as *P. euorientis* by Eitschberger (1983)

were published as a subspecies of *P. euorientis* (ssp. *mihon*) by Yakovlev (2006). Tadokoro et al. (2014) treated this taxon as *P. ochsenheimeri tianshansis* according to their phylogenetic results. However, it can be easily distinguished from *P. euorientis*, as the blackish apical spot is scattered and with a clear boundary without merg-

ing or suffusion (in *P. euorientis* grey and merging intra veins) and a mostly absent 1st discal spot (in *P. euorientis* mostly present but rather faint). After jointly observing the specimens of this study and a series of materials in Eitschberger (1983) and Tshikolovets (2009), we believe that the western population (populations around Tuva Republic and westwards) of the previously considered *P. euorientis* is *P. mihon*, while the eastern population (populations around Sayan Mountains and eastwards) is the real *P. euorientis* (Fig. 12). Although the molecular data of type specimens are lacking for phylogenetic analysis, this taxon can be morphologically distinguished from all similar species in the same regions. (e. g. the absence of all discal spot of males on the upperside). According to our phylogenetic results of Chinese specimens, this taxon was well defined as monophyletic and not clustering with *P. ochsenheimeri*. Combining the unique morphological characteristics of this taxon, until additional informative molecular evidence contradicts morphological results, we suggest that it should be treated as a distinct species, and therefore propose *P. ochsenheimeri tianshansis* as a new synonym for *P. mihon*.

Pieris dulcinea dulcinea (Butler, 1882)

Ganoris dulcinea Butler, 1882; Ann. mag. nat. Hist. (5) 9 (49): 18; TL: “Posiette Bay, Ussuri” [Posyet] (original description)

Pieris napi f. *dulcinea* (Butler, 1882); Seok (1941): Annotationes Zoologicae Japonenses 20: 105 (as subspecies of *Pieris napi* (Linnaeus, 1758))

Pieris dulcinea (Butler, 1882); Sheljuzhko (1960): Zeitschrift der Wiener Entomologischen Gesellschaft 45: 4–13, 20–29, 36–51 (as distinct species)

Description. Both wings white on the upperside and a pale yellowish hue (in summer forms whitish) on the underside. Spring form: small in size. Male (Fig. 9J): apical spot blackish, triangular, extending along veins to outer margin without merging. All discal spots absent or only the 1st discal spot faintly developed, outer spot absent or vague on the upperside. Outer edge of hindwing slightly black powdered along vein tips. Female (Fig. 9K): all veins narrowly brownish powdered on both sides. The 1st, 2nd and outer spot less distinctly present on both the upperside and underside, the 3rd spot absent. Summer form: large in size. Male (Fig. 9L): apical spot blackish, extending along veins to outer margin without merging. The 1st discal spot strongly developed on both sides while the 2nd discal spot faint on the upperside (but rather distinct on the underside). Dark powder along veins rather narrow on the underside. Outer spot less developed on the upperside and absent on the underside. Female (Fig. 9M): all veins rather narrowly brownish powdered on the upperside (relatively broader along outer margin of hindwings) while nearly absent on the underside. Apical spot dark brownish, extending along veins to outer margin without merging. The 1st and 2nd discal spot rather strongly developed on both sides while the outer spot distinct on the upperside but absent on the underside.

Distribution. Far East of Russia (Amur and Ussuri regions), Northeast China.

Phenology. Bivoltine from May to July.

Male genitalia. (Fig. 5L) tegumen broad with a distinct concave at almost its median part, distal margin of tegumen moderately-sclerotised as a pairs sub-lobe shaped convex; uncus with its basal width as wide as the distal part of tegumen, gradually tapering to a slender point.

Female genitalia. (Fig. 7B) posterior apophysis long and slender, extended beyond the 8th tergum; inner distal of sterigma short lobe shaped extend to center; inner basal of sterigma plate protrusion, rounded connected at the basal margin; signum cordiform-shaped with its terminal part broad and short, moderately tapering to the basal.

Note. This species rather resembles *P. euorientis* but can be distinguished by a comparison of morphological characteristics (see notes in *Pieris euorientis euorientis* Verity, 1908). This species is sympatric with *P. melete* while sometimes the spring forms of the two species may be confused. Spring forms of *P. dulcinea* can be distinguished from *P. melete* by having: males: discocell pure white without any grey or blackish powder (in *P. melete* grey powdered on the proximal part); females: apical spot and dark powder of veins relatively distinct (less developed in *P. melete*), all spots relatively narrower on the upperside (broader in *P. melete*).

Pieris erutae erutae Pujade, 1888

Pieris erutae Pujade, 1888; Bull. Soc. Ent. Fr. (6) 8: xix TL: “Mou-Pin” [Baoping, Sichuan] (original description)

Description: both wings white on the upperside and pale yellowish to yellowish on the underside. Spring form: medium size. Male (Fig. 10F, H): apical spot blackish with slightly whitish powder, merging as a small dark subtriangular spot on the apex. All discal spots and outer spots absent on the upperside (except for the 1st discal spot and outer spot sometimes rather faintly developed). The 2nd discal spot vaguely developed on the underside. Female (Fig. 10I): apical spot brownish, partly merging as a subtriangular spot on the apex. The 1st, 2nd and outer spot strongly developed as rectangular on the upperside while faintly present on the underside (except outer spot absent). All veins strongly brownish powdered on both sides especially forewings on the upperside. Summer form: medium to large size. Resembles spring form but larger with rounder wing shape. The 1st discal spot of males (Fig. 10G) present on both sides and the brown powder along veins is stronger in summer form of females (Fig. 10J, K) than spring forms.

Distribution. Central China (Sichuan, Chongqing, Yunnan, Guizhou, Qinghai), Thailand, Laos, Northern Vietnam, Myanmar.

Phenology. Bivoltine to multivoltine, occurs from April to August (October in Southern distribution areas).

Male genitalia. (Fig. 5M) tegumen broad, without distinct convex on the distal margin; basal margin of the uncus slightly narrower than tegumen, with its apical half of steeply digitation.

Female genitalia. (Fig. 7C) posterior apophysis slender, extended reach the 8th tergum; inner distal of sterigma lobe shaped extend to center; inner basal of sterigma broad strip shaped, without distinct convex, smoothly connected at the basal margin; signum cordiform shaped, smoothly tapering to the basal.

Pieris erutae reissingeri Eitschberger, 1983

Pieris erutae reissingeri Eitschberger, 1983; *Herbipoliana* 1(1–2): 374;

TL: “Hoeng-Shan (900 m), Provinz Hunan, China” [Hengshan Mountain, Hunan, China] (original description)

Pieris melete; Chou (1999): *Monographia Rhopalocerorum Sinensium* 1: 259, f6. [MisID]

Description. Both wings whitish on the upperside and yellowish on the underside. Spring form: medium size. Male: apical spot blackish with slightly whitish powdered, merging as a small dark subtriangular spot. All discal spots and outer spot absent on the upperside (sometimes the 1st discal spot and outer spot rather faintly developed). The 2nd discal spot vaguely developed on the underside or absent. Female (Fig. 10P): apical spot brownish, partly merging as a subtriangular spot on the apex. The 1st, 2nd and outer spot strongly developed, rectangular on the upperside while faintly present on the underside (except outer spot absent). All veins with strong brownish powder on both sides, especially forewings on the upperside. Summer form: medium to large size. Resembles spring form but larger with rounder wing shape. The 1st discal spot of males (Fig. 10Q) present on both sides and with distinct blackish powder along vein tips on the outer margin of hindwings on the upperside. The brown powder along veins is stronger in summer form of females (Fig. 10R) than spring forms.

Distribution. South China (Hunan)

Phenology. Multivoltine, occurs from April to September.

Male genitalia. (Fig. 5N) tegumen broad, without distinct convex on the distal margin; basal margin of the uncus slightly broader than tegumen, with its apical half of digitation.

Female genitalia. (Fig. 7D) posterior apophysis slender, almost reach the 8th tergum; inner distal of sterigma nearly spindle shaped extend to center; inner basal of sterigma broad pentagon shaped, smoothly connected at the basal margin; signum near cordiform shaped or near spindle shaped, indistinctly tapering to the basal.

Note. This subspecies rather resembles other *P. erutae* subspecies, while it can be distinguished only by the distinct dark powder along vein tips on the outer margin of hindwings on the upperside of summer forms of males.

Pieris erutae kneitzi Eitschberger, 1983 comb. rev.

Pieris erutae kneitzi Eitschberger, 1983; *Herbipoliana* 1(1–2): 378;

TL: “Tapaishan im Tsinling, Süd Shensi, China” [Taibai Mountain, Shaanxi, China] (original description)

Pieris dulcinea kneitzi; Tadokoro et al. (2014): *Butterflies* 65: 20. [MisID]

Description. Both wings pure white on the upperside and pale yellowish on the underside. Spring form: medium size. Male: Apical spot blackish and sometimes with slightly whitish powder, merging as a rather small dark subtriangular spot. All discal spots and outer spot absent on the upperside (sometimes the 1st discal spot and outer spot rather faintly developed). The 2nd discal spot vaguely developed on the underside or absent. Female: apical spot brownish, partly merging as a subtriangular spot on the apex. The 1st, 2nd and outer spot strongly developed in a rectangle on the upperside while faintly present on the underside (except outer spot absent). All veins with strong brownish powder on both sides, especially forewings on the upperside. Summer form: medium to large size. Resembles spring form but larger in size and with rounder wing shape. The apical spot of males (Fig. 10L, N) rather small and the 1st discal spot of males present on both sides. The brown powder along veins is stronger in summer form of females (Fig. 10M, O) than spring forms.

Distribution. Central west China (Shaanxi)

Phenology. Bivoltine, occurs from April to August.

Male genitalia. (Fig. 5O) tegumen relatively broad, without distinct convex on the distal margin; basal margin of the uncus slightly broader than tegumen, moderately tapering to a slender point.

Female genitalia. (Fig. 7E) posterior apophysis slender, extended reach the 8th tergum; inner distal of sterigma up-curved lobe shaped extend to center; inner basal of sterigma smooth quadrilateral shaped, smoothly connected at the basal margin; signum broad and shord, cordiform-shaped, distal margin obtusely concave and moderately tapering to the basal.

Note. This subspecies rather resembles other *P. erutae* subspecies, but can be distinguished by the smallest apical spot and slightest dark powdering along vein tips on the outer margin of hindwings on the upperside of summer forms of males. We noticed that this taxon was moved to *P. dulcinea* by Tadokoro et al. (2014) as *P. dulcinea kneitzi* because of a single specimen which clustered with

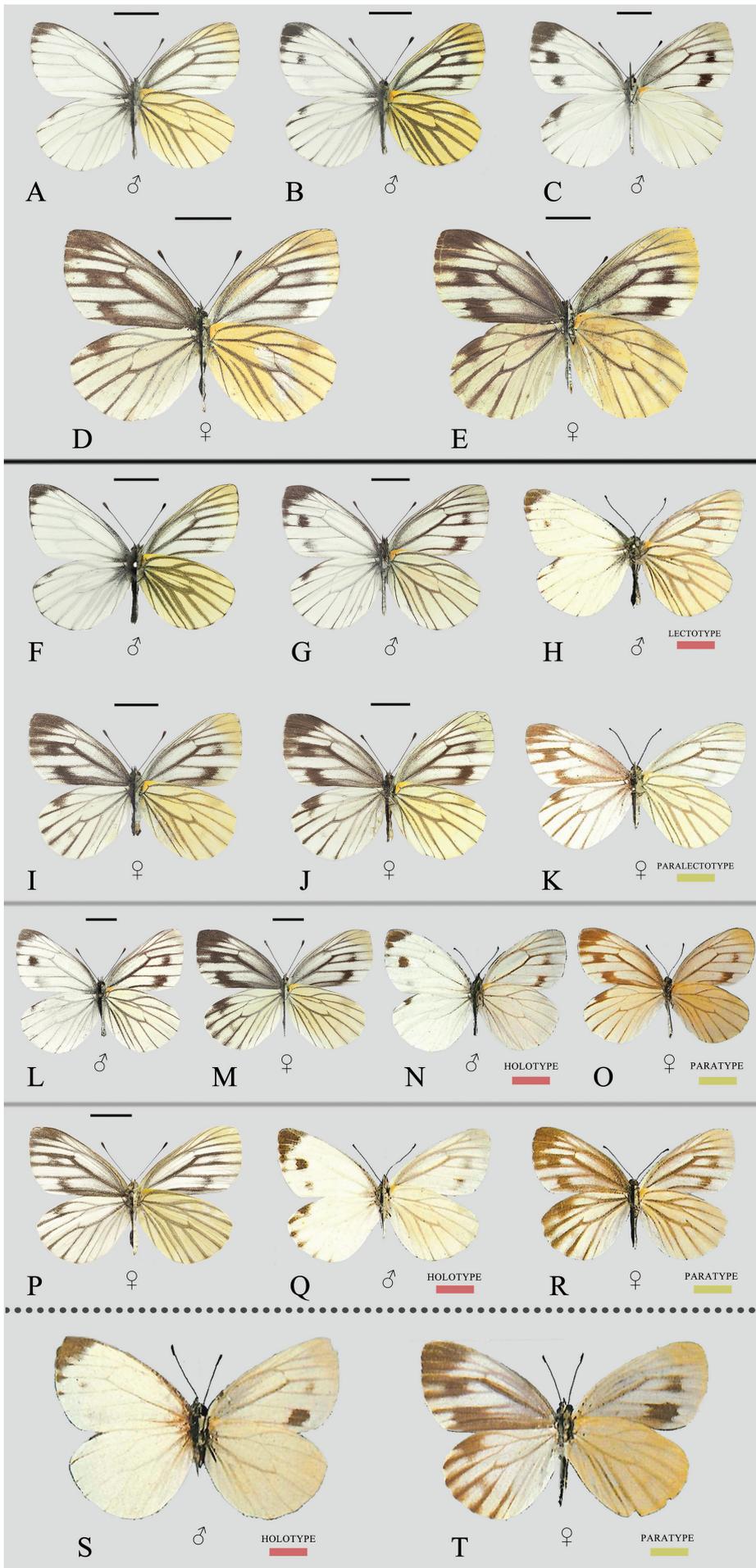


Figure 10. Habitus of *P. napi*-complex species occurring in China. Composite pictures on the left show the upper side, on the right show the underside. **A–E** *Pieris latouchei* Mell, 1939. **F–K** *Pieris erutae erutae* Pujade, 1888. **L–O** *Pieris erutae kneitzi* Eitschberger, 1983 comb. rev. **P–R** *Pieris erutae reissingeri* Eitschberger, 1983. **S–T** *P. steinigeri* Eitschberger, 1983. Scale bar represents 10 mm. (All type specimens reference Eitschberger, 1983).

P. dulcinea in their phylogenetic results. However, the author failed to describe any morphological difference that supported this, but indicated “the wing expanse is as large as *erutae* or *latouchei*.” Based on the collecting data of the sample which clustered with *P. dulcinea*: “China Wulingshan 07. 06. 9” and its note: “Specimens from Qingling-shan and beizing”, we suggest that this sample is very likely mislabelled, because “Wulingshan” (Wuling Mountain) is in east Beijing (which is a known habitat of *P. dulcinea dulcinea*), while “Qingling-shan” (Qinling Mountains) is the type locality of *P. dulcinea kneitzi*. These two different localities cannot be applied to a single sample, thus Tadokoro et al. (2014) probably mislabelled *P. dulcinea* as *P. e. kneitzi* and created a wrong combination.

Pieris latouchei Mell, 1939

Pieris extensa latouchei Mell, 1939; Dt. Ent. Z. Iris 52 (1938): 138–139.

TL: “Kuatun, NW-Fukien” [N.W. of Shaowu City, Fujian] (original description)

Pieris erutae latouchei; Eitschberger (1983): *Herbipoliana* 1(1–2): 376 (as subspecies of *Pieris erutae* Pujade, 1888)

Pieris melete latouchei; Wu (2010): *Fauna Sinica Insecta* 52: 300 (as subspecies of *Pieris melete* Ménétriés, 1857)

Pieris latouchei; Tadokoro et al. (2014): *Butterflies* 65: 25 (raised to distinct species from subspecies of *Pieris erutae*)

Description. Both wings white on the upperside while bright yellow on the underside (in autumn form males whitish). Spring form: medium size. Male (Fig. 10A): apical spot blackish with slightly whitish powder, merging as a small dark subtriangular spot on the apex. The 1st discal spot and outer spot rather faint or absent on the upperside. All spots absent on the underside, except the 2nd discal spot vaguely developed. Female: apical spot brownish, partly merging as a subtriangular spot on the apex. The 1st, 2nd and outer spot strongly developed on the upperside while faintly present on the underside (except outer spot absent). All veins narrowly brown powdered on both upperside and underside. Summer form: medium to large size. Resembles spring form but larger in size and rounder wing shape. The 1st discal spot of males (Fig. 10B) present on both sides and the brown powder along veins is stronger in summer form of females (Fig. 10D) than spring forms. Autumn form: large size. Male (Fig. 10C): resembles summer form but less yellowish on the underside (near whitish), the apical spot merging as a triangular spot and the 1st and 2nd discal spots rather distinct on both sides (the outer spot distinct on the upperside while absent on the underside). Female (Fig. 10E): resembles summer form but dark yellowish on the underside, all veins strongly brown powdered on the upperside while quite narrow on the underside.

Distribution. East China (Henan, Shandong, Jiangsu, Zhejiang, Fujian)

Phenology. Multivoltine, occurs from April to September.

Male genitalia. (Fig. 5K) tegumen relatively slender, with its median part slightly concave, the distal margin of tegumen without distinct convex; basal margin of the uncus slightly narrower than the tegumen; uncus with its apical obtusely digitation.

Female genitalia. (Fig. 7A) posterior apophysis slender, extended reach to the 8th tergum; inner distal of sterigma lobe-shaped, extend to center, with a distinct convex at the trailing edge; inner basal of sterigma near trapezoidal extend to the center, smoothly connected at the basal margin; signum cordiform-shaped, relatively slender, smoothly tapering to the basal.

Note. This taxon was elevated to species level by Tadokoro et al. (2014), based on results from his phylogenetic analysis, which is also supported by our molecular results. This species is closely related to *P. erutae* and shows three different seasonal forms in generations, thus can be only distinguished from the bright yellow color of wings on the underside (while in autumn forms are variable) and the basal 1/2 dark powdered discocell on the underside (only developed in autumn forms).

3.5. General profile of some species related to Chinese species of the *P. napi*-complex.

The most relevant species of the *P. napi*-complex distributed in adjacent regions of China are discussed and two European taxa (i.e. *P. napi napi* and *P. bryoniae wolfsbergeri*) are also included in this section in order to discuss the difference between them and East Asian species.

Pieris ochsenheimeri ochsenheimeri Staudinger, 1886

Pieris ochsenheimeri Staudinger, 1886; Stett. Ent. Ztg. 42: 199; TL: “Alai Mont.” [Namangan, Uzbekistan] (original description)

Description. Small in size. Both wings white on the upperside, and underside whitish or yellowish. Male (Fig. 11A): costal margin black; apical spot blackish, triangular, extending along veins to outer margin and sometimes partly merging apically. The 1st discal spot and outer spot distinct on both upperside and underside, while the 2nd discal spot only faintly present on the underside and the 3rd discal spot absent. Outer margin border of hindwings more or less blackish, sometimes triangularly extending along veins. Female (Fig. 11B): both wings intensive brownish or grey suffusion on the upperside, but clearly white in the apical half of discocell on the upperside of forewings. Outer margin border of hindwings blackish, sometimes with dark powered along veins. It should be also noted that there is another subspecies (i. e., *P. ochsenheimeri gerhardi* Eitschberger, 1983 which is mainly distributed in Peter I range in Tajikistan), that can be clearly identified as a subspecies of *P. ochsenheimeri* and will

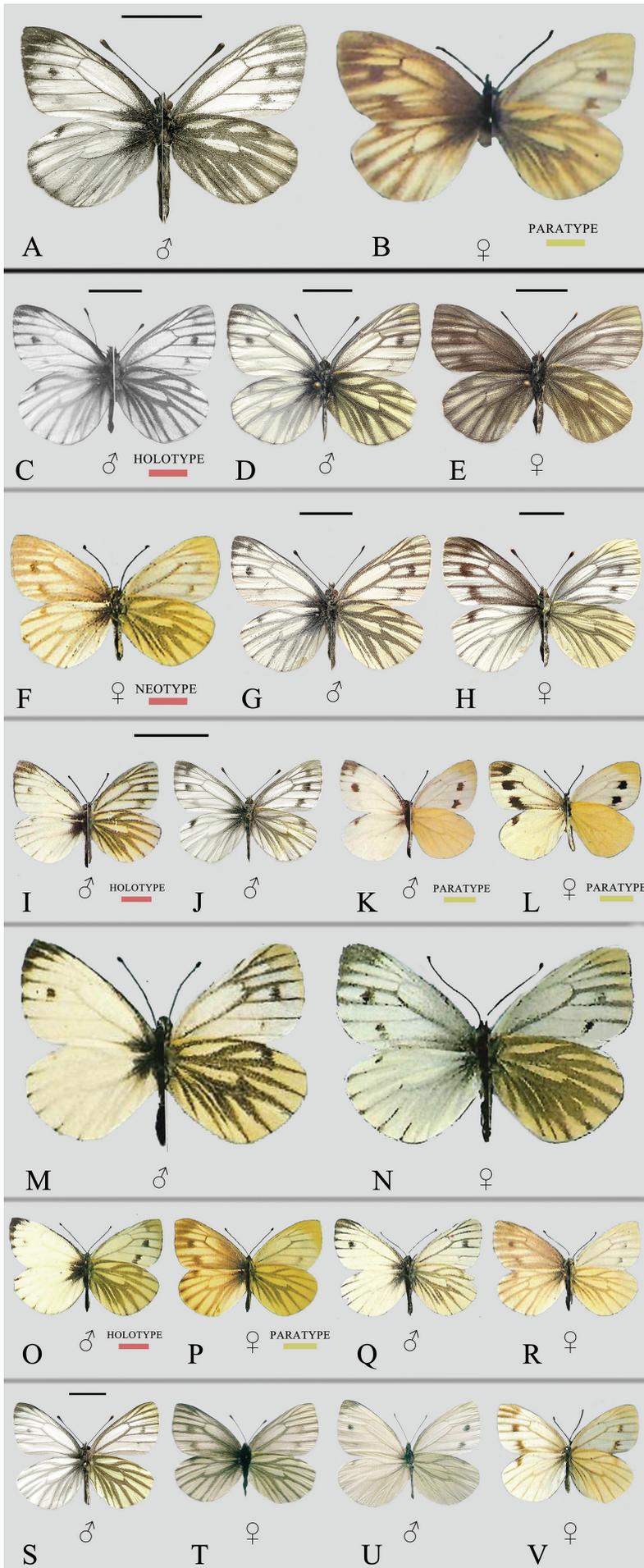


Figure 11. Habitus of species related to Chinese species of *napi*-complex. Composite pictures on the left show the upperside, on the right show the underside. **A–B** *Pieris ochsenheimeri ochsenheimeri* Staudinger, 1886. **C–E** *Pieris napi sauron* Yakovlev, 2004 comb. nov. **F–H** *Pieris napi bryonides* Sheljuzhko, 1910 comb. rev. **I–L** *Pieris napi muchei* Eitschberger, 1983. **M–N** *Pieris napi napi* (Linnaeus, 1758). **O–R** *Pieris bryoniae wolfsbergeri* Eitschberger, 1983. **S–V** *Pieris euorientis euorientis* Verity, 1908 stat. rev. Scale bar represents 10 mm. (B, F, I, K, L, O–R, V reference Eitschberger, 1983; T and U reference Tshikolovets et al., 2009; C reference Yakovlev, 2004 as black and white photos consistent with original description).

not be confused with other taxa. As we mainly focus on taxa that are easily confused with Chinese species, after confirming that *P. ochsenheimeri* does not occur in China, we will not further discuss ssp. *gerhardi* here.

Distribution. Uzbekistan, Kyrgyzstan, Tajikistan (Ghis-sar, Alai, western Tian-Shan).

Phenology. Unknown but occurs in June and July.

Male genitalia. (Fig. 5B) basal part of uncus almost as wide as terminal part of tegumen; uncus broad and moderately convex at its median part, apical half of uncus finger-shaped.

Female genitalia. Not examined.

Note. This species can be easily distinguished from others (except *P. narina*) by the relatively smaller size and the unique blackish markings on costal margin, apical spot of forewings and also outer margin border of hindwings on the upperside of males. While it can be distinguished from *P. narina* by the underside wing color (*P. ochsenheimeri* could be whitish or yellowish but *P. narina* always yellowish) and the males differ from *P. narina* by having the 1st discal spot distinct on the upperside (in *P. narina* absent or rather faint); females can be distinguished from *P. narina* by having forewing discocell clearly white in the apical half on the upperside (in *P. narina* completely brownish dusted or apically less than 1/3 whitish) and dark powder is usually less developed in *P. ochsenheimeri* compared to *P. narina* on the upperside.

Pieris napi napi (Linnaeus, 1758)

Papilio napi Linnaeus, 1758; Syst. Nat. (Edn 10) 1: 468; TL: Sweden (original description)

Description. Both wings white on the upperside, but with a pale yellowish (sometimes yellowish) hue on the underside. Male (Fig. 11M): apical spot blackish but sometimes powdered slightly whitish, merging as a dark triangle on the apex. The 1st discal spot and outer spot distinct to faintly developed, the 2nd discal spot absent on the upperside (but mostly faintly developed on the underside). The 3rd discal spot mostly absent. Female (Fig. 11N): grey or brownish powdered along veins; all discal spots and outer spot distinct except 3rd discal spot absent (a trend in some specimens). Apical spot variable, dark suffusion along veins but usually not merging inter-veins. Summer forms resembles spring forms but with a relatively larger size and more rounded wing shape. All spots of summer form are generally more developed than spring form.

Distribution. Europe

Phenology. Occurs from March to October, voltinism variable according to latitude and altitude.

Male genitalia. (Fig. 5C) terminal part of tegumen with a pair of lobes rising from its top, moderately convex and sclerotised, basal part of uncus almost as wide as terminal part of tegumen, gradually tapering to a slender point.

Female genitalia. (Fig. 6A) posterior apophysis long and slender, extended beyond the 8th tergum; sterigma with its inner distal short, lobe shaped extends to center; sterigma with its inner basal smoothly connected; signum cordiform-shaped, smoothly tapering basally with its margin irregularly concave.

Note. This species is widely distributed and could be very variable. Many taxa historically considered as belonging to this species may include other taxa, which need to be further studied by a combination of methods. The nominate subspecies was included in our phylogenetic analysis to clarify the taxonomic status of other taxa.

Pieris napi muchei Eitschberger, 1983

Pieris napi muchei Eitschberger, 1983; Herbiopoliana 1(1–2): 135; TL: “Kasachstan, Alatau, Almaarasan Umgeb., 1900–2100 m” (original description)

Description. Both wings pure white on the upperside, and bright yellow on the underside. Spring form: male (Fig. 11I, J): apical spot blackish, triangular, extending along veins to outer margin without merging or suffusion. The 1st, 3rd and outer spot distinct (2nd discal spot absent and 3rd discal spot sometimes faint) on the upperside. Summer form: male (Fig. 11K): both wings clearly whitish without dark powder along veins, the 1st discal spot and outer spot strongly developed and the 3rd discal spot merging with the apical spot as a square on the upperside. The 1st and 2nd discal spot distinct on the underside. Females (Fig. 11L) resemble males but with all dark markings more developed.

Distribution. East Kazakhstan; Kyrgyzstan; Uzbekistan; Tajikistan

Phenology. Flies from April to September, bivoltine or trivoltine (Tuzov et al., 1997).

Male genitalia. (Fig. 5F) terminal part of tegumen without lobe shaped convex; basal part of uncus slightly narrowed as terminal part of tegumen; uncus moderately convex at its median part.

Female genitalia. Not examined.

Note. This subspecies can be easily distinguished from all other taxa distributed in the same region by the mostly distinct 3rd discal spot on the upperside and bright yellow color on the underside. The whitish wings without any dark powder of the summer form also make this subspecies very easy to identify. Unfortunately, we did not find

any female specimens of its spring form. Future field surveys are essential to clarify this issue.

***Pieris napi sauron* Yakovlev, 2004 comb. nov.**

Pieris euorientis sauron Yakovlev, 2004; Helios 5: 233, pl. 16, f. 1–8; TL: “East Kazakhstan, Saur Mts, Chagan-Obo, 1600–1800 m, 47°02N, 84°54E” (original description)

Description. Male (Fig. 11C, D): both wings white on the upperside, but yellowish on the underside. Apical spot blackish with an inward suffusion. Outer margin border blackish from apical spot to vein CuA_2 . The 1st discal spot mostly present but more or less faint. The 2nd and 3rd discal spot absent or only indicated on the upperside (The 2nd discal spot mostly present on the underside but rather faint). Outer spot on the hindwing present but faint. Outer margin border blackish. Female (Fig. 11E): both wings intensively brownish or grey suffusion on the upperside, especially forewings. Forewing underside with a grey hue but yellowish apically, hindwing underside dark-yellowish. The 1st and 2nd outer spot distinct, and the 3rd discal spot usually present on the upperside, but all spots (except absent outer spot) faintly present on the underside.

Distribution. East Kazakhstan (Saur Mountains)

Phenology. Unknown but occurs in June.

Male genitalia. (Fig. 5D) tegumen narrow and long, terminal part moderately sclerotised as almost lobe-shaped convex; basal part of uncus distinctly narrowed as terminal part of tegumen; uncus with steeply convex at its median part and averagely tapering to the end.

Female genitalia. (Fig. 6B) posterior apophysis short and slender, almost reach the 8th tergum; inner distal of sterigma lobe shaped, almost contact in the center; inner basal of sterigma with distinct convex; signum cordiform shaped, broad at the terminal margin and moderately tapering to the basal.

Note. This taxon was first published as a subspecies of *P. euorientis* Verity, 1908. However, in the original description, the author did not claim any morphological characteristics that show the taxon belongs to *P. euorientis*. In fact, this subspecies is morphologically different from *P. euorientis*, and the morphological characteristics of males rather similar to those of *P. napi*. Females of this taxon are morphologically very close to some subspecies of *P. napi* (e.g. *P. napi adalwinda* Fruhstorfer, 1909). Our phylogenetic results indicate that this taxon belongs to *P. napi*. Although the *P. napi* subspecies show great morphological variability, it is more appropriate to classify this taxon as a subspecies of *P. napi*.

***Pieris napi bryonides* Sheljuzhko, 1910 comb. rev.**

Pieris napi var. *bryonides* Sheljuzhko, 1910; Rev. russ. ent. 9: 384; TL: “Umg. Dscharkent, Ili Geb.” [Zharkent, Kazakhstan] (original description)

Pieris bryoniae bryonides; Eitschberger (1983): Herbiopoliana 1(1–2): 122 (as subspecies of *Pieris bryoniae* (Hübner, 1805))

Pieris bryoniae ab. *heptopotamica* Krulikovsky, 1904; Eitschberger (1983): Herbiopoliana 1(1–2): 122 (nom. nud.)

Description. Both wings white on the upperside, but pale yellowish to bright yellowish on the underside. Male (Fig. 11G): apical spot blackish or brownish, triangular, extending along veins to outer margin without merging. The 1st discal spot mostly distinct as rounded. The 2nd discal spot absent and the 3rd discal spot rather slightly developed on the upperside (the 2nd discal spot distinct on the underside). Outer spot on the hindwing rather faint or absent. Female (Fig. 11F, H): both wings moderately brownish or grey suffusion on the upperside, especially area around humeral angle of forewings. The 1st, 2nd and outer spot distinct, and the 3rd discal spot usually absent or faintly developed on the upperside, but only 1st and 2nd discal spot faintly present on the underside.

Distribution. East Kazakhstan (N. Tian-Shan, Dzhungarsky Alatau)

Phenology. Unknown but occurs from May to July

Male genitalia. (Fig. 5E) terminal part of tegumen moderately sclerotised as almost lobe-shaped convex; basal part of uncus slightly narrower as terminal part of tegumen with its median part slightly convex, apical half of uncus digitation.

Female genitalia. (Fig. 6C) posterior apophysis short and relatively robust, almost reaches the 8th tergum; inner distal of sterigma lobe-shaped, almost contact in the centre; inner basal of sterigma without distinct convex, smoothly connect in the basal margin; signum cordiform shaped, short and slender, smoothly tapering to the basal.

Note. This taxon was formerly considered as a subspecies of *P. bryoniae* by Eitschberger (1983) as the “females strongly resembled the summer generations of southern alpine *bryoniae*.”. Our phylogenetic results indicate that this taxon is distantly separated from *P. bryoniae wolfsbergeri* from the Alps but is more closely related to *P. napi*. Although the only description given to this taxon originally was “female which are very grey (powdered).”, based on the Neotype, as both wings are grey-powdered on the upperside, it is rather cleanly-whitish when compared to *P. bryoniae wolfsbergeri* and other subspecies. Combined with our molecular results, we believe that this taxon is more appropriately classified as a subspecies of *P. napi*.

Pieris bryoniae wolfsbergeri Eitschberger, 1983

Pieris bryoniae wolfsbergeri Eitschberger, 1983; *Herbipoliana* 1(1–2): 154; TL: Piemonte, Italy (original description)

Description. Spring form: male (Fig. 11O): both wings white on the upperside and a pale yellowish hue on the underside. Apical spot blackish, sub-triangularly extending along veins to outer margin with moderately suffusion, sometimes reached vein CuA_2 . The 2nd and 3rd spot completely absent while the 1st and outer spot faintly developed to absent on the upperside. Underside with the 1st, 2nd and 3rd spot distinct to rather faintly developed, outer spot variable. Female (Fig. 11P): both wings pale yellowish to yellowish with intensively brownish suffusion on the upperside while yellowish on the underside, but clearly in the apical 2/5 of discocell on the upperside of forewings. Hindwings with dark powder moderately developed along veins. Summer form: male (Fig. 11Q): both wings clearly whitish with dark powder moderately developed along veins on the underside, the 1st discal spot distinctly developed and the outer spot moderately present while other spots absent to rather faintly developed on both sides. Females (Fig. 11R) both wings with intensively brownish or grey suffusion on the upperside while pale yellowish on the underside; upperside with the 1st, 2nd and outer spot distinctly developed and a trend of 3rd spot; discocell on the upperside of forewings almost full of dark suffusion. Hindwings with dark powder developed along veins.

Distribution. Italy (S. W. Alps)

Phenology. Bivoltine from June to September

Male genitalia. (Fig. 5G) tegumen broad on the basal part while moderately narrower extends to the terminal

part; basal part of uncus slightly narrower as terminal part of tegumen with its median part slightly convex, apical half of uncus digitation.

Female genitalia. (Fig. 6F) posterior apophysis comparatively robust; inner distal of sterigma slightly up-curved extend to center; inner basal of sterigma setose, acute-angled connected at the basal margin; signum with its apical cordiform part elongated, moderately tapering to the basal.

Note. This taxon was included in our phylogenetic analysis to clarify its relationship with morphologically similar taxa distributed in China and adjacent regions. In fact, this taxon occurs far away from East Asia. Our results also show that East Asian taxa can be clearly distinguished from this taxon.

Pieris euorientis euorientis Verity, 1908 stat. rev.

Pieris napi var. *euorientis* Verity, 1908; *Rhopalocera Palaearctica* (13–14): 147, (17–20): pl. 32, f. 44; TL: “Sajan” (original description)

Pieris euorientis Verity, 1908; Eitschberger (1983): *Herbipoliana* 1(1–2): 131 (upgraded as distinct species)

Pieris dulcinea euorientis; Tuzov et al. (1997) (as subspecies of *Pieris dulcinea*)

Pieris napi euorientis; Tadokoro et al. (2014): *Butterflies* 65: 26 (as subspecies of *Pieris napi*)

Description. Both wings white on the upperside and a pale yellowish hue on the underside. Male (Fig. 11S, U): apical spot grey, merging as a small dark subtriangular spot on the apex or nearly absent. The 1st discal spot and outer spot present but rather faint on both upperside and underside, while the 2nd spot vaguely developed on the

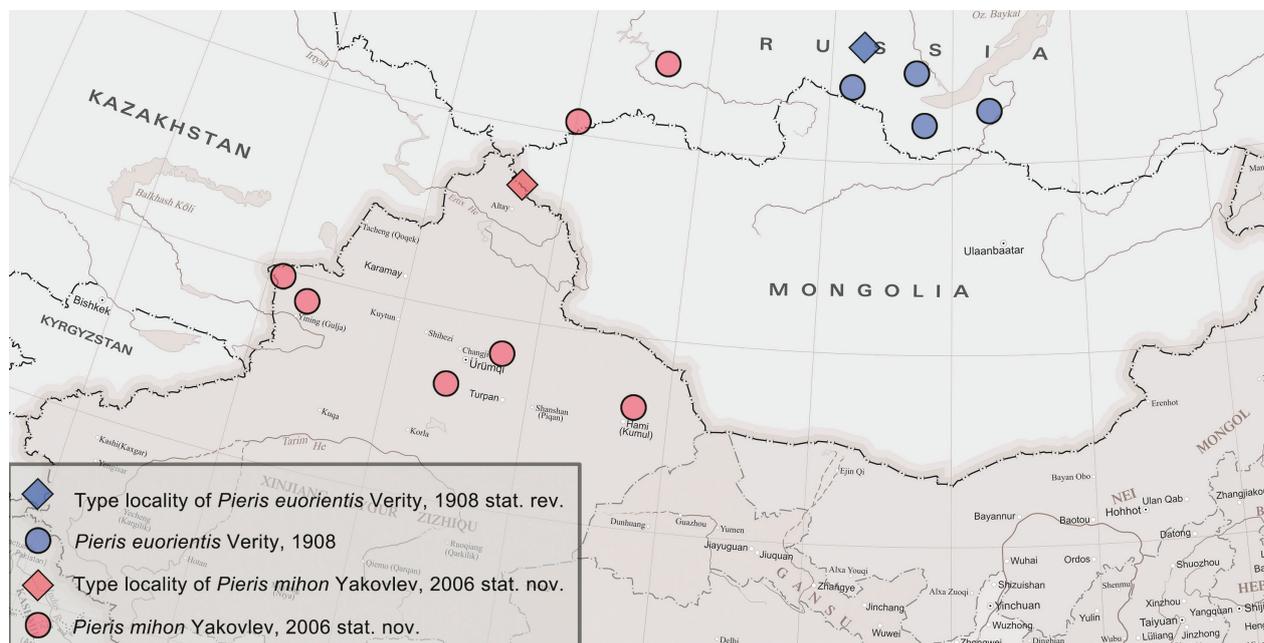


Figure 12. Distribution map of *Pieris euorientis* Verity, 1908 stat. rev. and *Pieris mihon* Yakovlev, 2006 stat. nov.

underside. Female (Fig. 11T, V): all spots distinctly developed on the upperside, while relatively faint on the underside. Brownish or blackish powder distinctly narrowed along all veins on both sides, relatively broader at the apex.

Distribution. Russia, Mongolia (Altai and Sayan Mts, Siberia and Transbaikalia)

Phenology. Univoltine from June to July (Tuzov et al., 1997).

Male genitalia. (Fig. 5J) basal part of uncus moderately narrower than the distal margin of tegumen, as a concave between uncus and tegumen; uncus slightly convex at its median part, apical half of uncus digitation.

Female genitalia. Not examined.

Note. This species rather resembles the spring form of *P. dulcinea* which can only be distinguished by a comparison of the apical spot (more or less merging in this species while always separated into several triangles in *P. dulcinea*) and the 1st discal spot (both species faint but in *P. euorientis* relatively more developed). Males can be easily distinguished from the summer form of *P. dulcinea* in having: apical spot merged (separate in *P. dulcinea*), and 1st discal spot faint (strongly developed in *P. dulcinea*) and 2nd discal spot absent (present in *P. dulcinea*) on the upperside. This taxon shows monophyly in our phylogenetic analysis and its position is distant from *P. napi*; therefore, we consider this taxon to be a distinct species. It is noteworthy that in the re-description of the species by Eitschberger (1983) a series of specimens from Tanu-Ola (Tanguura Mountains) were considered as belonging to this species, while in this study, we found morphological differences between topotypes of *P. euorientis* and specimens from regions south or west of the Tanguura Mountains (See notes in *Pieris mihon* Yakovlev, 2006 stat. nov.). Combined with our phylogenetic results, this indicates that populations from the Tanguura Mountains and the regions to the south or west represent a distinct species (Fig. 12): *Pieris mihon* Yakovlev, 2006 stat. nov. As the redefined *Pieris euorientis euorientis*, we did not find female specimens of the summer form in the type locality or adjacent regions, thus this knowledge gap needs to be filled in future research.

3.6. Revision of other taxa similar to the *P. napi*-complex occurring in China

Pieris melaina Röber, 1907

Pieris melaina Röber, 1907; Gross-Schmett. Erde 1: 48, pl. 20 g; TL: "Tibet" (original description)

Pieris melaina melaina Röber, 1907; Eitschberger (1983): *Herbipoliana* 1(1–2): 406 (pictured)

Pieris melete melete ra. *montana* Verity, 1908; Eitschberger (1983): *Herbipoliana* 1(2): 406–408 (as a synonym of *P. melaina*)

Pieris melaina Röber, 1907; Tadokoro et al. (2017): *Lepidoptera Science*: 68(3–4): 81–91 (pictured)

Description. Both wings whitish on the upperside while pale yellowish on the underside. Male (Fig. 13A, C): apical spot blackish and sickle shaped. The 1st discal spot distinct and almost combined with the apical spot, the 2nd discal spot absent or faintly developed on the upperside while distinct on the underside. The outer spot distinct on the upperside while absent on the underside. Female (Fig. 13B, D): extremely dark powdered along veins on the upperside, with the 1st and 2nd discal spot merging with the apical spot, thus brownish suffusion on almost all outer marginal area except slightly whitish area in the space between vein CuA₂ and 2A.

Distribution. East Tibet (Yadong, Bomi), India (border to Tibet)

Phenology. Univoltine in high altitude habitat (occurs in July and August above 4000 m) while probably bivoltine in low altitude habitat (occurs in April and July below 3000 m).

Male genitalia. (Fig. 5A) tegumen broad, distinctly convex on its 4/5 apically; basal part of uncus moderately convex and with its apically distinctly narrowed towards tip.

Female genitalia. (Fig. 8A) sterigma with its inner distal bilobate lobe-shaped, shallowly expended to the centre; inner basal of sterigma arcuately protruding, smoothly connected at the basal margin; signum variable, cordiform to near cordiform-shaped.

Pieris extensa Pujade, 1888

Pieris erutae var. *extensa* Pujade, 1888; Bull. Soc. Ent. Fr. (6) 8: xix; TL: "Moupin, China" [Baoping County, Sichuan] (original description)

Description. Extremely large in size, especially summer form males (Fig. 13E) (females with a relatively smaller size of males). Both wings white on the upperside while a creamy yellow hue on the underside. Male (Fig. 13E): apical spot blackish and sickle shaped. The 1st discal spot distinct and divided in the middle part, the 2nd discal spot rather faintly developed on the upperside while distinct on the underside. All veins rather narrowly blackish powdered, except vein M₃ and Rs strongly powdered. The outer spot strongly developed and merging with the blackish powdered vein Rs, thus reaches the outer margin on the upperside while rather faintly developed on the underside. Female (Fig. 13F): resembles male but all dark patterns brownish and the 2nd discal spot more developed;

outer margin of hindwings rather strongly brownish powdered along veins, with a suffusion faintly developed as an outer margin band on the upperside.

Distribution. South China (Zhejiang, Sichuan, Shaanxi, Yunnan)

Phenology. Bivoltine, from May to July.

Male genitalia. (Fig. 5P) tegumen extremely broad with its median part slightly concave, the distal margin of tegumen without distinct convex; basal margin of the uncus as wide as the distal margin of tegumen; uncus broad with its apical gradually tapering to a obtusely point.

Female genitalia. (Fig. 8B) posterior apophysis slender, extended reach the 8th tergum; inner distal of sterigma spindle shaped extend to center; inner basal of sterigma plate protrusion extend to the center, smoothly connected at the basal margin; signum cordiform shaped, with extremely broad transparent central axle.

Pieris chumbiensis gyantsensis Verity, 1911

Pieris dubernardi var. *chumbiensis* r. *gyantsensis* Verity, 1911; Rhopalocera Palaearctica (30–36): 329, pl. 66, f. 21–23; TL: “Gyangtse, S. Tibet” (original description)

Synchloe chumbiensis gyantsensis; Bollow (1930): The Macrolepidoptera of the World, supplement to Vol. 1: 339 pp, pl.16. (infrasubspecific name validated as subspecies of *Synchloe chumbiensis*)

Pieris gyantsensis; Tadokoro et al. (2014): Butterflies 65: 33 (as distinct species)

Pieris chumbiensis gyantsensis; Tadokoro et al. (2016): Lepidoptera Science 67: 99–114

Pieris chumbiensis gyantsensis; Huang (2019): Neue Entomologische Nachrichten 77: 203–255 (pictured, keyed)

Description. Medium size. Both wings whitish on the upperside while yellowish on the underside. Male (Fig. 13G): apical spot blackish, triangular extending along veins to outer margin with a trend of merging. A short black band at the end of the discocell. The 1st spot distinct and oval-shaped, with a trend of a spot faintly occurs on the cell between vein CuA₁ and CuA₂; outer spot less faintly present on the upperside. All veins of hindwings heavily brownish powdered on the underside, with a brownish sub-outer marginal band. Female (Fig. 13H): resembles male but with black markings more developed. The 1st spot distinctly developed and extends as a black band reaching the posterior margin. Hindwings with blackish sub-marginal band distinctly developed on both sides.

Distribution. Tibet (from Lhasa to Nyalam)

Phenology. Univoltine, occurs in June and July.

Male genitalia. (Fig. 5Q) tegumen broad with its distal margin slightly narrower; basal margin of uncus slightly

convex with a moderate concave between tegumen and uncus; uncus with its median part slightly convex, apical half of uncus digitation.

Female genitalia. (Fig. 8C) posterior apophysis long and slender, extended beyond the 8th tergum; inner distal of sterigma lobe shaped extend to center; inner basal of sterigma without distinct convex, smoothly connected at the basal margin; signum short and broad, almost disk shaped with smooth and shallowly concave on the terminal margin; basal part of signum tubular with distinct bending on the most basal part.

Note. The taxon *gyantsensis* was originally published by Verity (1911) as a quadrimomial race belonging to *P. chumbiensis*, thus unavailable due to being infrasub-specific. When Bollow (1930) re-defined this taxon as a subspecies of *Synchloe chumbiensis*, the subspecies name became an available name. This taxon was once mistreated as belonging to the *P. napi*-complex by Tadokoro et al. (2014) according to their phylogenetic results and observations on androconial characteristics. Our molecular results oppositely showed that this taxon constitutes a distinct molecular lineage separated from the *P. napi*-complex. Moreover, this taxon has long been considered as a member of the *P. dubernardi*-group, a unique species group with distinctive morphological characteristics and a high altitude habitat which includes *P. dubernardi*, *P. rothschildi*, *P. wangi* as well as *P. chumbiensis*.

Pieris melete melete Ménétriés, 1857

Pieris melete Ménétriés, 1857; Cat. lep. Petersb. 2: 113, pl. 10, f. 1–2; TL: Japan (original description)

Pieris napi var. *orientis* Oberthür, 1880; Etud. d'Entom. 5: 13; TL: Asakold.

Pieris orientis Oberthür, 1880; Eitschberger (1983): Herbiopliana 1(1–2): 339 (upgraded as distinct species from *Pieris napi* var. *orientis*)

Pieris napi; Chou (1999): Monographia Rhopalocerorum Sinensium 1: 258, f5. [MisID]

Pieris orientis Oberthür, 1880; Tadokoro (2011): Butterflies 58: 34–40 (as a synonym of *Pieris melete melete*)

Pieris orientis Oberthür, 1880; Wu & Hsu (2017): Butterflies of China vol.1: 404, f. 17–18

Description. Both wings whitish on the upperside and pale yellowish to yellowish on the underside. Spring form: medium size. Male (Fig. 13I): apical spot blackish with slightly whitish powder, partly merging as a small dark triangular spot on the apex. All discal spots and outer spot absent on the upperside or only the 1st discal spot faintly developed. The 1st and 2nd discal spot vaguely developed on the underside. Female (Fig. 13J): apical spot brownish without suffusion or merging. The 1st, 2nd and outer spot present on the upperside while only the 2nd discal spot present on the underside. All veins with rather narrowly brownish powder on both sides. Summer form: medium to large size. Resembles spring form, but larger in size and with rounder wing shape. Male (Fig. 13K):

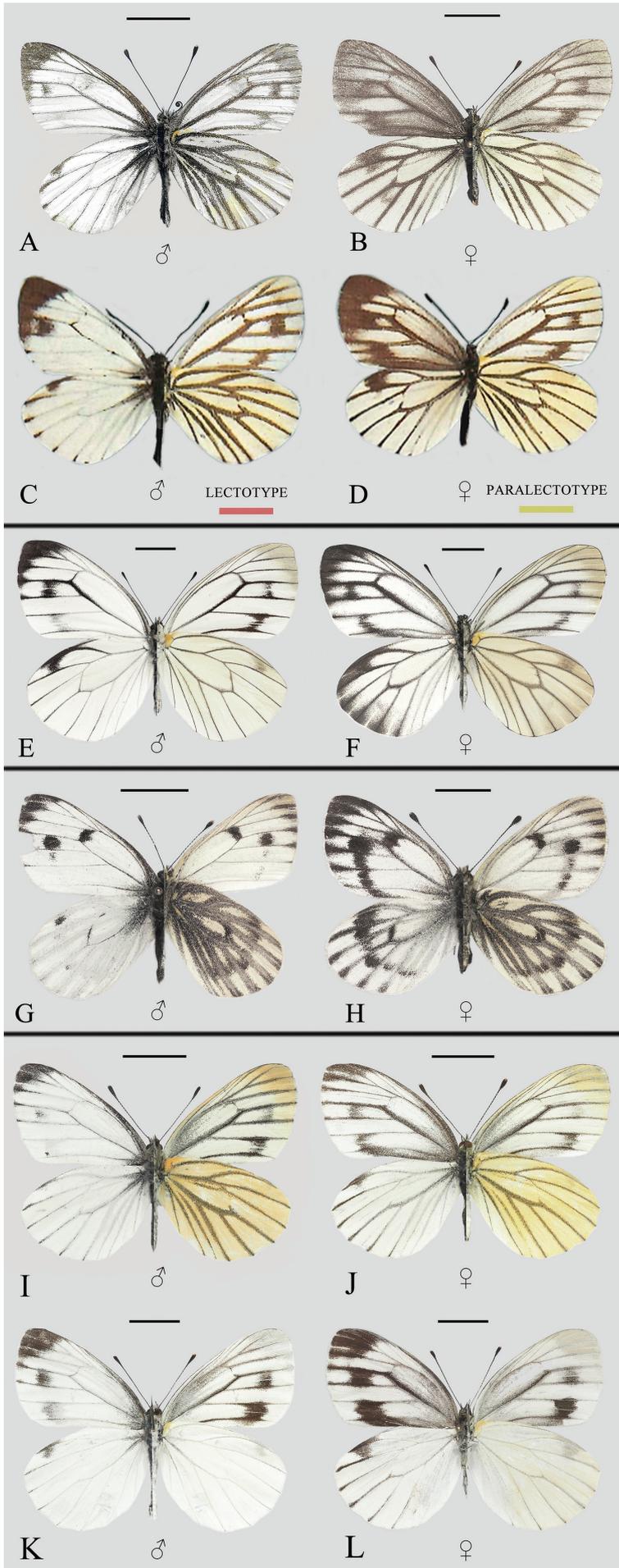


Figure 13. Habitus of species similar to the *P. napi*-complex, distributed in China. Composite pictures on the left show the upperside, on the right show the underside. **A–D** *Pieris melaina* Röber, 1907. **E–F** *Pieris extensa* Pujade, 1888. **G–H** *Pieris chumbiensis gyantsensis* Verity, 1911. **I–L** *Pieris melete* Ménétriés, 1857. Scale bar represents 10 mm. (C, D reference Eitschberger, 1983)

the 1st discal spot present on both sides and the 2nd discal spot strongly developed on the underside (sometimes also rather faintly developed on the upperside). Female (Fig. 13L): all spots strongly developed on both sides (except the outer spot absent on the underside). Dark powder along veins less developed than spring forms in both sexes and almost absent on the underside of hindwings.

Distribution. Northeast China, North and South Korea, Japan, Far East Russia

Phenology. Bivoltine, from May to August.

Male genitalia. (Fig. 5R) tegumen broad on its basal part and narrower in the apical half; basal margin of uncus as wide as the distal margin of tegumen with a slight concave intermedia; uncus with its median part moderately convex, apical half of uncus digitation.

Female genitalia. (Fig. 8D) inner distal of sterigma near spindle shaped with its distal part distinct expanded; inner basal of sterigma plate protrusion, acutely-angled connected at the basal margin; signum cordiform shaped, extremely short and broad, with its terminal margin smoothly obtusely concave.

Note. It is noteworthy that the eastern Russian and Chinese populations of this taxon were elevated to species level by Eitschberger (1983) (*i. e.*, *Pieris orientis*) and the recent Chinese work, Wu & Hsu (2017), followed the abovementioned viewpoint. However, Tadokoro (2011) based on phylogenetic analysis of specimens from a relatively wide range of regions treated this taxon as a synonym of *Pieris melete melete*. Here we follow the opinion of Tadokoro (2011).

4. Discussion

In this study, we examined all currently recognized species and most taxa historically considered as belonging to the *P. napi*-complex from China and its adjacent regions. Five Chinese species of the *P. napi*-complex have been identified: namely *P. latouchei*, *P. dulcinea*, *P. erutae*, *P. narina*, and *P. mihon*, of which the latter two species are new records for China. Our phylogenetic analysis indicates that nine of the species considered in this study belong to the *P. napi*-complex. This result agrees with previous studies to a great extent as *P. extensa*, *P. melaina* and *P. melete* were excluded from the complex (Eitschberger 1983; Tadokoro et al. 2013). However, contrary to the research of Tadokoro et al. (2013), our phylogenetic results show that *P. chumbiensis gyantsensis* is not a member of the *P. napi*-complex. This taxon belongs to the *P. dubernardi*-group, which has a special adaptation to high altitudes. It is noteworthy that according to our results, *P. melaina* is sister to all *P. napi*-complex species and appears to be more closely related with the *P. napi*-complex

than with *P. melete* according to the K2P distances (about 2.5% to the *P. napi*-complex while 5% to *P. melete*) or the phylogenetic tree constructed by the 16S rDNA gene (Figure S2) (clustered as sister to the species of *P. napi*-complex but distant from *P. melete*). However, *P. melaina* has been excluded from the *P. napi*-complex judging from its form of androconia (which is closely related to *P. melete*), as originally classified by Warren (1961), and we suggest that *P. ajaka* may be closely related to *P. melete* and *P. melaina*. Thus we excluded *P. melaina* from the *P. napi*-complex.

In addition, two taxa which have been reported from China were absent from our specimen collections: *Pieris steinigeri* Eitschberger, 1983 (TL: Weihsi 2400 m [Weixi County, Yunnan]) and *P. bryoniae sifanica* Grum-Grshimalio, 1895 (TL: Amdo [Qinghai]). If the former is a true species, the only *P. napi*-complex species recorded as sympatric is *P. erutae*. The holotype of *P. steinigeri* shows unique morphological characteristics (Fig. 10S): a rather faintly developed 1st discal spot, a strongly developed 2nd discal spot on the underside, a half dusted discocell on the underside of forewings and the darkish stripe along veins almost absent. The above features are often exhibited in *P. erutae* individuals in a similar although not identical way. Nevertheless, we still do not consider *P. steinigeri* to be a distinct species. Weihsi County is a popular collection locality, but individuals of *P. steinigeri* other than the type specimens have not been recorded from here for decades. On the other hand, the absence of a darkish stripe along veins is always exhibited by the autumn forms of *P. erutae*, which occurs in late September and October, thus a rarely selected collecting time. Therefore, we speculate that *P. steinigeri* may be a special variation of the autumn form of *P. erutae*. However, further confirmation may require more detailed sample collection. For the latter, the type locality of Amdo (the old name of Qinghai) is large and vague. Similarly, *P. erutae* is also recorded in the southeast of Qinghai. Interestingly, we found specimens identified as *Pieris bryoniae sifanica* from Xinjiang and Qinghai on a European butterfly website (http://www.euroleps.ch/seiten/s_art.php?art=pier_bryoniae&modus=). A specimen from Qinghai labelled as “China, Qinghai, Caka 60km w Heimaha 3500–4500 m, 6.–12. Juli 1991, leg. V. PAULUS. Männchen” looked no different from a spring form of *P. erutae*; and specimens labelled as “China, Xinjiang, Borohoro-Shan 1600–3100 m,” can be easily identified as *P. mihon*. Although we speculate that *P. bryoniae sifanica* may be a synonym of *P. erutae*, we cannot make a conclusion before examining the type specimens. However, it is certain that this taxon is more likely to belong to *P. napi* than to *P. bryoniae*, due to its rather eastern distribution compared to that of other subspecies of *P. bryoniae*.

Notably, at the subspecies level, *P. erutae* failed to show monophyly in our phylogenetic analysis. Whether these subspecies have their own territories with definite boundaries requires further investigation. Although their morphological differentiation can only be observed in some seasonal types (usually difficult to distinguish in spring forms), we currently still adopt the taxonomic

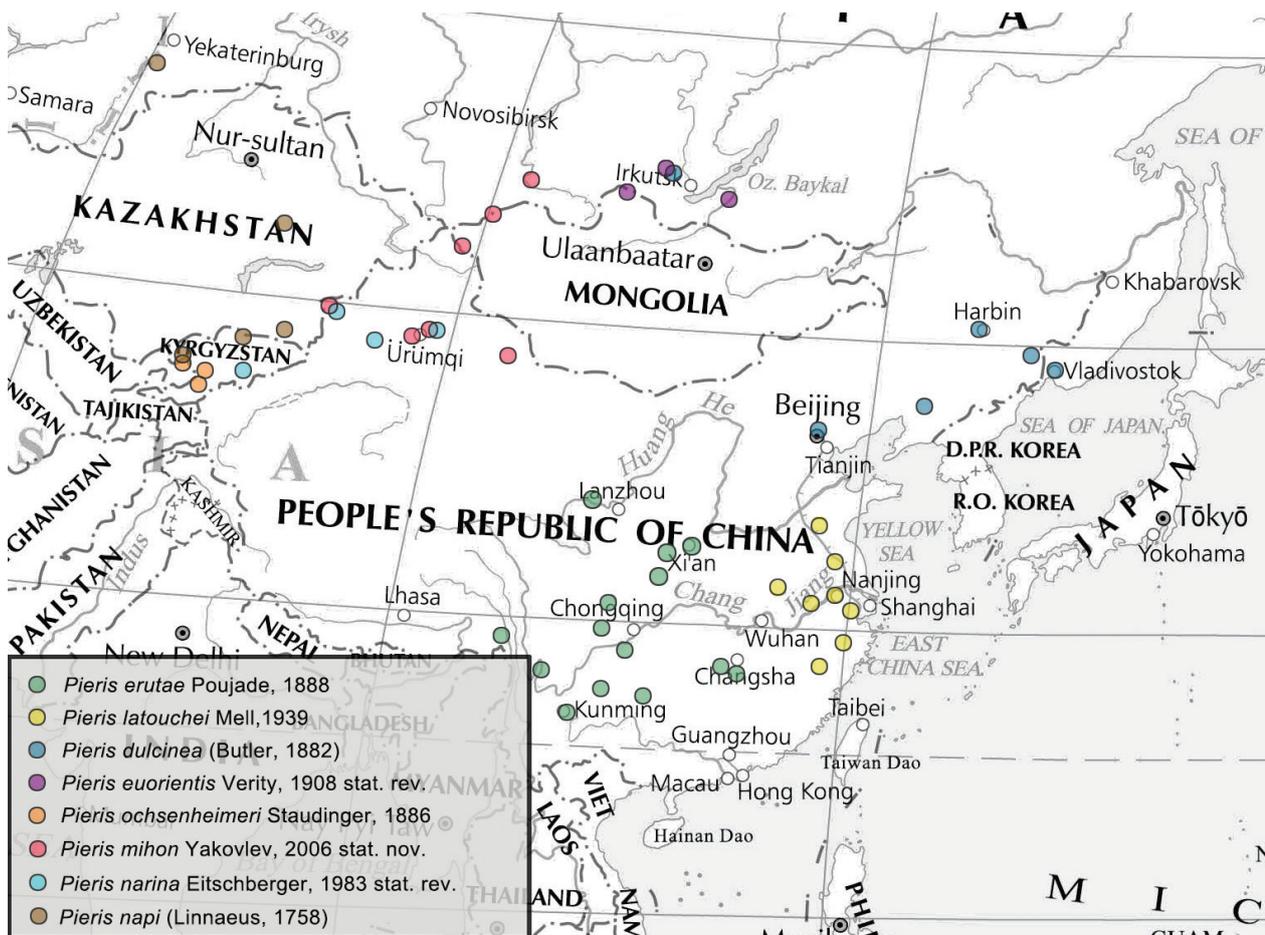


Figure 14. Distribution map of *Pieris napi*-complex species distributed in China and adjacent regions.

opinions of Eitschberger (1983) and list them as separate subspecies, before further evidence becomes available. Moreover, the K2P distances between species distributed in East China and East Russia (e.g., *P. euorientis*, *P. latouchei*, *P. dulcinea*) are very small. However, these species can be easily distinguished by morphological and biological characteristics. We speculate that these species may have been formed by rapid diversification in a short time and incomplete lineage sorting as well as gene introgression may also occur in such closely related species. As most of the genes we employed in our phylogenetic analysis were mitochondrial (4 of the 6 analyzed genes), they would certainly dominate the phylogeny in a combined analysis. However, nearly all samples (except for outgroups) were paraphyletic in the phylogenetic tree reconstructed with the nuclear *Wingless* gene (Figure S3). Although the 16S rDNA gene may distinguish species out of the *P. napi* complex to a certain extent, its resolution within the complex is still limited (Figure S2). Species of the *napi*-complex and other members of the genus are often found to be the dominant species in their respective distribution areas, with few reported examples of sympatry (at least on a local scale). For example, *P. rapae* is the dominant species in cities in southern China, while *P. erutae* is dominant in suburban areas, indicating that taxa of the *P. napi*-complex and also other *Pieris* species differ in their ecological niches. These ecological niche differences may be the result of differences in climatic conditions,

environmental factors and host preferences, thus reducing the competition of related species and ensuring the dominant position of the genus in a vast geographical range.

In this study, a series of specimens from China and its adjacent areas were examined. After detailed study, we concluded that the shape of the valve in male genitalia was not suitable for species identification, due to high individual variability. We also did not employ the morphology of androconia to distinguish the relevant taxa, because characters of androconia show conspicuous individual and geographical variations and are highly homogeneous in several taxa. Tadokoro et al. (2013) and Eitschberger (1983) also indicated that the androconial morphology may always show distinct difference between species groups, while it is difficult to distinguish within the species of the *napi*-complex. In fact, the distribution and wing patterns are very important for the identification of species in the *P. napi*-complex. Although these species and subspecies have diverse seasonal forms, their identifications are usually feasible if based on a series of specimens. In this study, we focused on the taxonomy of the *P. napi*-complex in China and its adjacent regions. However, as a widely distributed group, further studies are still needed on the species and subspecies which are distributed in Europe, America and Africa. The interspecific and subspecies classification based on geometric morphology and multispectral methods may provide an updated and more in-depth perspective.

5. Author Contributions

Si-Xun Ge: Conceptualization (lead); data curation (lead); formal analysis (lead); methodology (lead); resources (lead); software (lead); visualization (supporting); funding acquisition (equal); writing original draft (lead). Zhuo-Heng Jiang: formal analysis (equal); software (equal); data curation (supporting); visualization (lead). Jia-Qi Wang, Kui Song and Chao Zhang: data curation (supporting); resources (equal); Shao-Ji Hu: project administration (lead); resources (equal); supervision (lead); funding acquisition (equal); validation (lead); writing review and editing (lead).

6. Acknowledgements

We gratefully acknowledge Adam M. Cotton (Chiang Mai, Thailand) for his comments and great help in improving the earlier drafts of this article. We thank Prof. Chun-Sheng Wu (Institute of Zoology, CAS, Beijing, China), Dr. Hao Huang (Qingdao, China), Dr. Hong-Liang Shi (College of Forestry, Beijing Forestry University), Dr. Xin-Yu Li (College of Forestry, Beijing Forestry University) and Dr. Han Xu (College of Forestry, Beijing Forestry University), Mr. Hao-Han Mao (College of Forestry, Beijing Forestry University) for their great support for this study. Finally, we thank Teruo Tadokoro, Vladimir Lukhtanov and two anonymous reviewers for comments on the manuscript. We would also like to thank the editor Martin Wiemers for his thoughtful comments on the manuscript. The authors declare no conflicts of interest. This study was funded by the China BON-Butterflies of the Ministry of Ecology and Environment of P. R. China (SDZXWJZ01013).

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Supplementary material 1

Table S1

Authors: Ge SX, Jiang ZH, Wang JQ, Song K, Zhang C, Hu SJ (2023)

Data type: .xlsx

Explanation note: Detail informations of specimens used in molecular analysis.

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Link: <https://doi.org/10.3897/asp.81.e85191.suppl1>

Supplementary material 2

Figure S1

Authors: Ge SX, Jiang ZH, Wang JQ, Song K, Zhang C, Hu SJ (2023)

Data type: .jpg

Explanation note: Ladderized phylogenetic tree reconstructed with combined genes.

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Supplementary material 3

Figure S2

Authors: Ge SX, Jiang ZH, Wang JQ, Song K, Zhang C, Hu SJ (2023)

Data type: .jpg

Explanation note: Phylogenetic tree reconstructed with the ribosomal 16S gene.

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Supplementary material 4

Figure S3

Authors: Ge SX, Jiang ZH, Wang JQ, Song K, Zhang C, Hu SJ (2023)

Data type: .jpg

Explanation note: Phylogenetic tree reconstructed with the nuclear gene wingless.

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