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(Lepidoptera: Papilionidae)**

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► **To cite this version:**

Hui-Hong Zhang, Adam M Cotton, Fabien L. Condamine, Rong-Jiang Wang, Yu-Feng Hsu, et al..
Revision of Pazala Moore, 1888: The Graphium (Pazala) alebion and G. (P.) tamerlanus Groups,
with Notes on Taxonomic and Distribution Confusions (Lepidoptera: Papilionidae). *Zootaxa*, 2020,
4759 (1), pp.77-97. 10.11646/zootaxa.4759.1.5 . hal-03035162

HAL Id: hal-03035162

<https://hal.science/hal-03035162v1>

Submitted on 2 Dec 2020

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Revision of *Pazala* Moore, 1888: The *Graphium* (*Pazala*) *alebion* and *G. (P.) tamerlanus* Groups, with Notes on Taxonomic and Distribution Confusions (Lepidoptera: Papilionidae)

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Abstract

Three *Graphium* species belonging to two species groups of the subgenus *Pazala*, the *alebion* and *tamerlanus* groups, were examined in molecular and morphological studies, and their female genitalia are reported for the first time. Their relationship with other species groups within the subgenus is assessed and their divergence times are estimated. We find that *G. (P.) alebion* is the first lineage to diverge within *Pazala* in the early Miocene (20 Ma) and that *G. (P.) tamerlanus* and *G. (P.) parus* are sister species and diverged from each other in the late Miocene (7 Ma). A revision of the four recognised taxa belonging to three species is presented, and historical misidentification of these taxa and their geographic ranges are explained.

Keywords: male genitalia; female genitalia; geographic range; morphological confusion; divergence time

Introduction

The *Graphium* (*Pazala*) *alebion* and *G. (P.) tamerlanus* groups are two species groups of subgenus *Pazala* Moore, 1888 as defined by Hu *et al.* (2018). They currently consist of only three species, namely *G. (P.) alebion* (Gray, [1853]) in the *alebion* group; and *G. (P.) parus* (Nicéville, 1900) and *G. (P.) tamerlanus* (Oberthür, 1876) in the *tamerlanus* group. Both groups are in relatively 'primitive' phylogenetic positions compared to the *mandarinus*, *eurous*, and *mullah* groups (Hu *et al.* 2018). The shared morphological characters include a single, non-bifurcated hindwing discal band ("8"-shaped in the *mandarinus* group, double paralleled in the *eurous* group, and posteriorly bifurcated in the *mullah* group), as well as simple, smaller, triangular- or pear-shaped dorsal terminal harpe in the male valvae (Racheli & Cotton 2009). However, the female genitalia of these three species, which can provide new insights in taxonomy of *Pazala*, have not been systematically described and compared to date.

During the taxonomical revision of subgenus *Pazala*, we carefully re-examined the types of all these three species as well as other available materials in the Natural History Museum (BMNH, London, UK) and the Höne collection of the Zoologisches Forschungsinstitute und Museum Alexander Koenig (ZFMK, Bonn, Germany). Freshly collected specimens were also carefully examined, dissected, and used for molecular phylogenetic analyses. Although our analyses did not discover any cryptic species or new subspecies like the preceding studies (Hu *et al.* 2018; Hu *et al.* 2019), some note-worthy historical, taxonomic, and distributional confusion in museum collections and literature were discovered.

The aims of the present study are the reconstruction of phylogenetic relationships of known species and subspecies of the two groups, estimation of molecular divergence times of all recognised taxa of the two groups, and comparison of male and female genitalia. A distribution map and notes addressing the taxonomic and distributional confusions are discussed after the systematic study.

Materials and Methods

Taxon sampling

A large number of specimens of all taxa in the *alebion* and *tamerlanus* groups were examined and sampled from the authors' private collections, other private collections and specimen depositories of academic institutions, with permission. A list of all the examined materials of taxa in the *alebion* and *tamerlanus* groups, including type specimens, together with the names and abbreviations of depositories, is given in Appendix 1 at the end of this work. Subspecific designations for *Pazala* species followed Racheli & Cotton (2009).

Morphological comparison

Freshly obtained specimens were spread for examination, with the scent scales on their hindwings exposed.

Spread specimens were photographed using a digital camera with medium grey background. Photos were adjusted using Adobe Photoshop CS (Adobe, USA). For comparison between taxa, the lengths of forewing were measured to 0.5 mm precision. Average lengths of forewing were calculated, and the standard deviations were also calculated when $n \geq 3$.

To observe the male and female genitalia, the abdomen was removed from the specimen and placed into a 1.5 mL microcentrifuge tube, and 1 mL water was added to the abdomen to rehydrate the tissue at 50 °C for 30 min, then 1 mL 10% sodium hydroxide solution was used to digest soft tissue at 70 °C for 1 h. The treated abdomen was neutralised with 2% acetic acid and then dissected in a water-filled Petri dish under the stereoscope to remove residual tissues, scales, and hair. The genitalia were then transferred to 80% glycerol for 12 h to render them transparent. Photographs were taken with a Nikon DMX1200 digital camera (Nikon, Japan) mounted on a Nikon SMZ1500 stereoscope (Nikon, Japan) and automatically stacked using Helicon Focus 3.2 (Helicon Software, USA). The median distance between the bases of socii of male genitalia (marked in Fig. 4) is a useful morphometric character, helpful to distinguish species (Koiwaya 1993); this distance, therefore, was measured to 0.2 mm precision for all dissected male genitalia. After observation and photography, all parts of the genitalia were fixed on a card with water soluble white glue and pinned with the specimen. The terminology of male and female genitalia followed Hu *et al.* (2018).

Molecular work

For specimens used in molecular work, one or two legs (except forelegs) on the same side were extracted, homogenised in protease buffer containing 100 μ L STE (10 mmol/L Tris-HCl, 1 mmol/L EDTA, 100 mmol/L NaCl, pH = 8.0) and 2 μ L Proteinase K (20 mg/mL) (O'Neill *et al.* 1992). Homogenised samples were treated at 37 °C incubation for 15 min to rehydrate the tissue and then at 95 °C incubation for 10 min to lyse the tissue. The supernatant was recovered through centrifugation at 6,000g and used directly as DNA template in polymerase chain reactions (PCR).

The PCR was executed in a 25 μ L system by using TaKaRa Ex Taq Kit (TaKaRa Biotechnology Co., Ltd., Dalian, China) that contained 2.5 μ L of 10 \times PCR buffer, 2.0 μ L of MgCl₂ (25 mmol/L), 2.0 μ L of dNTP mixture (2.5 mmol/L each), 0.25 μ L of Taq DNA polymerase (5 U/ μ L), and 0.5 μ L of each of forward and reverse primers (20 μ mol/L). We sequenced the mitochondrial barcode COI (cytochrome oxidase subunit I, *cox1*) with the following primers LCO1490 (5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3') and HCO2198 (5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3') (Folmer *et al.* 1994). The thermal profile of PCR consisted of an initial denaturation at 95 °C for 3 min; 30 cycles of denaturation at 94 °C for 1 min, annealing at 50 °C for 1 min, and elongation at 72 °C for 1 min; then a final elongation at 72 °C for 5 min. Sequences were obtained by using an ABI Prism 3730 sequencer (Applied Biosystems, California, USA).

Phylogenetic analyses

Raw sequences were proofread and aligned using Clustal W (Thompson *et al.* 1994) in BioEdit 7.0.9 (Hall 1999), and any sequence containing double peaks in the chromatograms was strictly excluded. The product sequences were checked by MEGABLAST against the genomic references and nucleotide collection in NCBI. Amino acid translation was realised with the invertebrate mitochondrial criterion in MEGA 6.0 (Tamura *et al.* 2013) to detect possible *Numts* (nuclear copies of mtDNA fragments). A search for nonsynonymous mutations, in-frame stop codons, and indels was carried out to further minimise the existence of cryptic *Numts* (Song *et al.* 2008; Bertheau *et al.* 2011). Sequences used in the present study were listed in Table 1.

The phylogeny was reconstructed using Bayesian Inference (BI) method as implemented in MrBayes 3.2.6 (Ronquist *et al.* 2012), with the most appropriate partition scheme recovered by PartitionFinder 2.1.1 (Lanfear *et al.* 2017) using the *unlinked* branch lengths and the *greedy* algorithm. We used the partitioning scheme and among-site rate variation suggested by PartitionFinder, but instead of selecting one substitution model *a priori*, we used reversible-jump Markov Chain Monte Carlo (rj-MCMC) to allow sampling across the entire substitution rate model space (Huelsenbeck *et al.* 2004). BI analyses consisted of two independent runs, each with eight rj-MCMC running for 10 million generations (sampled every 1000th generation) to calculate the clade posterior probabilities (PP).

As in Hu *et al.* (2018), we used an individual of *Iphiclides podalirius* (Linnaeus, 1758) and of *Lamproptera meges* (Zinken, 1831), because we found that tree topology and node support were improved when using outgroup species that branched before *Pazala*. We reconstructed the phylogeny for a dataset containing the currently recognised species of *Pazala* (*sensu* Hu *et al.* 2018) in an attempt to obtain an overall phylogenetic framework for the subgenus and to produce phylogenetic relationships among the focal taxa in the present study.

Phyletic properties of each taxon in the *alebion* and *tamerlanus* groups were assessed using an online tool, Monophylizer (Mutanen *et al.* 2016; <http://monophylizer.naturalis.nl/>). Taxa identified as monophyletic were treated as good species or subspecies, while those identified as paraphyletic were further analysed using morphological characters and geographical ranges.

Molecular dating

To estimate divergence times and infer their 95% credibility intervals (CI), we performed Bayesian relaxed-clock analyses using MrBayes. For these analyses, we relied on the partitioning scheme and all the MrBayes settings as determined above. Dating analyses were realized with two independent runs for 20 million generations with sampling tree every 2,000 generations. We used the autocorrelated clock model (noted TK02 in MrBayes) for two reasons. First, the autocorrelated model is more appropriate for our dataset because the rate along a given branch is more similar to its parent branch than a branch chosen at random, though autocorrelation models differ in the degree to which they restrict rate variation between parent and daughter branches (Thorne *et al.* 1998; Thorne & Kishino 2002). Second, Lepage *et al.* (2007) and Rehm *et al.* (2011) showed that the autocorrelated clock model generally offers the best fit, as compared to the uncorrelated model and a strict molecular clock model. Unlike previous dating analyses on *Pazala* (Hu *et al.* 2018, 2019), which relied on the TK02 clock model, better dating results were obtained in the present study using the IGR clock model.

Calibration priors are based on the time-calibrated tree of Papilionidae (Condamine *et al.* 2012). We set four secondary calibrations using a (conservative) uniform prior with bounded by the minimum and maximum ages of the 95% CI of the divergence times (a normal prior is not recommended, Schenk 2016). We could not use fossils in this study because the three fossils do not belong to the subfamily Papilioninae (Condamine *et al.* 2012). We calibrated the following nodes: (i) the root of the tree (crown of Leptocircini) set between 27.6 and 43.4 million years ago (Ma); (ii) the crown between *Iphiclides* and *Lamproptera* set between 20.8 and 35.5 Ma; (iii) the crown of the genus *Graphium* set between 21.2 and 35.7 Ma; and (iv) the crown of the subgenus *Graphium* set between 14.4 and 29.7 Ma. Following Hu *et al.* (2018, 2019), *Graphium agamemnon* (KC970100) and *G. sarpedon* (KF401961) were added to the molecular dataset to better calibrate the molecular clock.

For all Bayesian runs (phylogenies and dating), convergence was ensured by checking average deviation of split frequencies (ADSF), potential scale reduction factor (PSRF) values, effective sample size (ESS) of all parameters, and by plotting log-likelihood of samples against number of generations in Tracer 1.7 (Rambaut *et al.* 2018). To reach good convergence, the runs must have values of ADSF approaching zero, PSRF close to 1.00 and ESS above

200. Bayesian consensus trees were obtained using the 25% burn-in criterion (Ronquist *et al.* 2012), and the remaining samples were used to generate a 50% majority rule consensus tree.

All phylogenetic and dating analyses were performed on the computer cluster CIPRES Science Gateway (Miller *et al.* 2015), using BEAGLE (Ayres *et al.* 2012) with default parameters.

Results

Phylogenetics of the *alebion* & *tamerlanus* groups

Bayesian phylogenetic analyses converged well as indicated by ADSF close to 0, PSRF equal to 1, and ESS >> 200 for all parameters. The corresponding phylogeny of the *alebion* and *tamerlanus* groups showed that species were well defined as monophyletic with high (if not maximal) posterior probabilities (Figure 1). Confirming previous works (Hu *et al.* 2018), we found *G. (P.) alebion* as the sister species to all *Pazala* groups, including the *tamerlanus* group containing *G. (P.) parus* and *G. (P.) tamerlanus*. In the *G. (P.) tamerlanus* branch, two subspecies, namely ssp. *tamerlanus* and ssp. *kansuensis*, are identified.

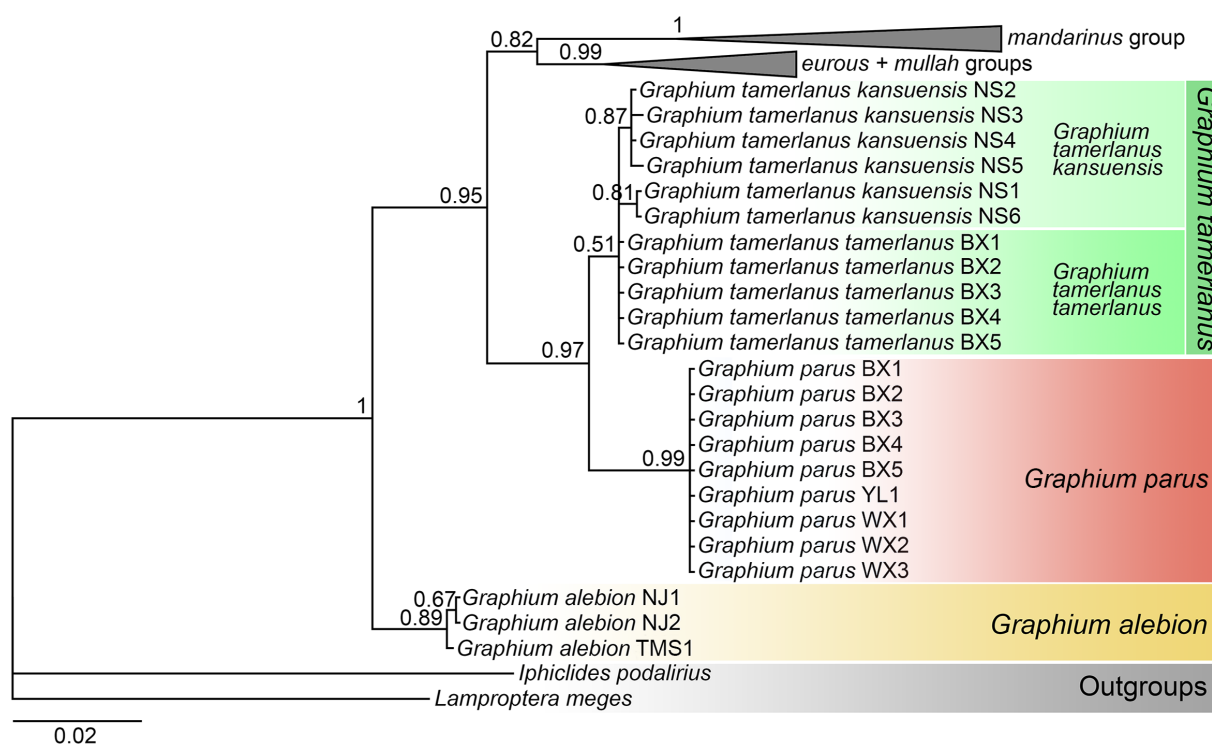


FIGURE 1. The Bayesian phylogenetic tree of the *Graphium (Pazala) alebion* and *G. (P.) tamerlanus* groups, with *Iphiclides podalirius* and *Lamproptera meges* as outgroup. Coloured rectangles delineate the species and subspecies of the two groups. Values at nodes indicate the posterior probability.

The Monophylizer analysis identified all three species in the two groups as monophyletic, while *G. (P.) tamerlanus kansuensis* entangled (but not mixed) with *G. (P.) tamerlanus tamerlanus* forming a paraphyletic clade in the tree (Table 2). The phylogenetic structure and Monophylizer assessment of the two groups indicate the following two taxonomic results: (i) all three species are distinct species, differing from each other in the tree; (ii) *G. (P.) tamerlanus kansuensis* is genetically rather close to the nominate subspecies of *G. (P.) tamerlanus*, but is morphologically a good subspecies.

The Kimura 2-parameter (K2P) distances (in percentage) between taxa ranged from 0.31% to 6.55%, with that between *G. (P.) tamerlanus tamerlanus* and *G. (P.) tamerlanus kansuensis* being the smallest, while that between *G. (P.) alebion* and *G. (P.) parus* being the greatest. In agreement with the so-called barcoding gap (Meyer & Paulay 2005), all K2P distances between identified species were greater than 2% (Table 3).

TABLE 2. Monophyly assessment of species and subspecies in the *Graphium (Pazala) alebion* and *G. (P.) tamerlanus* groups.

Taxon	Assessment	Tanglees
<i>G. (P.) alebion</i>	monophyletic	—
<i>G. (P.) parus</i>	monophyletic	—
<i>G. (P.) tamerlanus</i>	monophyletic	—
ssp. <i>tamerlanus</i>	paraphyletic	ssp. <i>kansuensis</i>
ssp. <i>kansuensis</i>	paraphyletic	ssp. <i>tamerlanus</i>

TABLE 3. The Kimura 2-parameter distances (shown in percentages) between species and subspecies in the *Graphium (Pazala) alebion* and *G. (P.) tamerlanus* groups.

Taxon	1	2	3a	3b
1. <i>alebion</i>				
2. <i>parus</i>	6.55			
3a. <i>tamerlanus tamerlanus</i>	5.54	2.01		
3b. <i>tamerlanus kansuensis</i>	5.66	2.33	0.31	

Revision of the *alebion* & *tamerlanus* groups

Graphium (Pazala) alebion (Gray, [1853]) (Figure 3)

Papilio alebion Gray, [1853]; Cat. lepid. Ins. Coll. Br. Mus., 1: 30, pl. 13, f. 6; TL: ‘Northern China’ [probably S. of Shanghai, China].

Papilio Mariesii Butler, 1881; Ann. Mag. nat. Hist. (Ser. 5), 7: 33, t. 4, f. 4; TL: ‘Lu-Shan mountains, province of Kiukiang, China’ [Lu Shan, Jiujiang, Jiangxi, China].

Cosmodesmus hönei O. Bang-Haas, 1927; Horae Macrolepid., 1: 1. [nomen nudum, published in synonymy]

Cosmodesmus hoenei O. Bang-Haas, 1927; Horae Macrolepid., 1: 1. [nomen nudum, published in synonymy]

Diagnostic characters: Small in size, forewing length: male 31.0–33.5 mm (mean = 32.1 ± 1.0 mm, $n = 4$), female 33.5–35.0 mm (mean = 34.1 ± 0.6 mm, $n = 4$). Both wings distinctively narrow and elongate, ground colour with a light ochreous hue. Forewing the 1st, 2nd, 8th, 9th black bands and the terminal (10th) black band all reach tornal margin in both sexes; area between the 8th and 9th bands almost devoid of dark scales; the 7th band not displaced inward in cell R₄; veins CuA₂ to M₂ stained with black distally. Hindwing discal band broadened towards costa; a whitish small patch at the base of tail in cell M₃; tornal yellow spots large and undivided on both sides.

Nomenclatorial note: The type specimen in BMNH was labelled as ‘Lectotype’ by Campbell Smith with the intention of designating it as such in a subsequent revision, similar to the type of *Papilio glycerion* Gray, 1831 (Hu *et al.* 2018). A literature search confirmed that this specimen has not actually been formally designated as the lectotype, and since Gray did not state the number of specimens when he described *Papilio alebion* the specimen must be treated as a syntype. Since there is no clear reason requiring lectotype designation in this case, we refrain from doing so in this publication.

Distribution: E. China (Zhejiang, Jiangxi, Jiangsu, Anhui, Hunan).

Phenology: Univoltine in mid-March to early April.

Host plant: *Lindera rubronervia* (Lauraceae) is reported in Nanjing, Jiangsu (Zhang *et al.* 2018). Host plant usage in other parts of its distribution range needs further study.

Male genitalia (Figure 4): Five male genitalia in total were dissected, and the general characters were consistent. Highly sclerotized. Ring slightly wavy in the upper half; saccus rather reduced; socius acute and smooth, distance between the base of socii 0.48–0.52 mm (mean = 0.50 ± 0.01 mm, $n = 5$). Valve short, oval in general, mostly dark in colour except for the base (unique in subgenus *Pazala*); dorsal terminal harpe triangulate, edge serrate with the base widely separated apart; the medial harpe long and nearly straight, the dorsal projection almost flat, broader at the base and gradually narrowed into a pointed tip; no tooth in the middle of the medial harpe. Aedeagus shorter than the other species, almost straight. Juxta very small and narrow, highly sclerotized without hair, the base not directly associated with the base of valves.

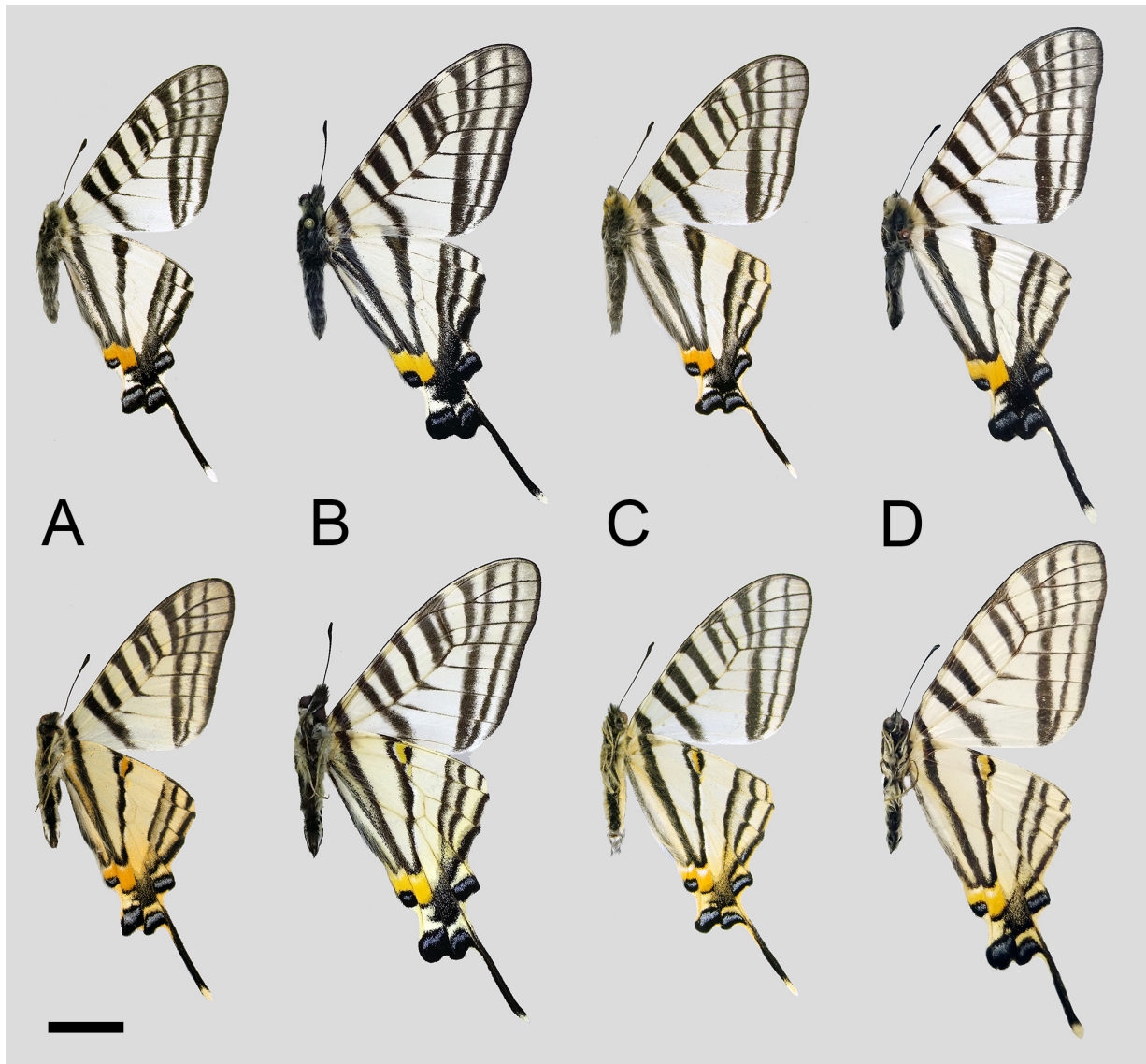


FIGURE 3. *G. (P.) alebion* (Gray, [1853]); upperside above, underside below; scale bar = 10 mm. A–B: ♂, Nanjing, Jiangsu, China; C: ♀, ditto; D: ♀, Jurong, Jiangsu, China; A and C © Jian-Qing Zhu (Shanghai Zoological Park, Shanghai, China).

Female genitalia (Figure 5): In total, three females were available for dissection, and the characters were consistent. Lamella postvaginalis very reduced; lamella antevaginalis broad horizontally; ostial lobe heavily sclerotized, broad at the base and gradually narrowed into a blunt tip in lateral view, while the posterior margin smoothly wavy without any indentation or bifurcation in ventral view.

***Graphium (Pazala) parus* (Nicéville, 1900) (Figure 6)**

Papilio parus Nicéville, 1900; J. Bomb. nat. Hist. Soc., 13 (1): 172, pl. EE, f. 21; TL: ‘Tse Kou, Western China’ [Yanmen (in the upper Lancang-Mekong valley), Deqen, N.W. Yunnan, China].

Cosmodesmus tamerlanus incertus O. Bang-Haas, 1927, Horae Macrolepid., 1: 1, pl. 5, f. 3; TL: ‘China mer. occ.: Szetschwan, Tatsienlu, Tsekou, Siaolu’ [Kangding, Yanmen, and Washan, Sichuan, SW. China].

Cosmodesmus tamerlanus taliensis O. Bang-Haas, 1927, Horae Macrolepid., 1: 2, pl. 5, f. 4; TL: ‘China mer. occ.: Jünnan, Tali’ [Dali, Yunnan, SW. China].

Pazala incerta Chou, 1994; Monographia Rhopalocerorum Sinensium: 55, 176. [unjustified emendation]

Pazala eurous Leech; Lee, 1995; Yunnan Butterflies: 51 (f. 65, n. 4). [misidentification]

Pazala tamerlanus Oberthür; Lee, 1995; Yunnan Butterflies: 51 (f. 67, n. 2), 140. [misidentification]

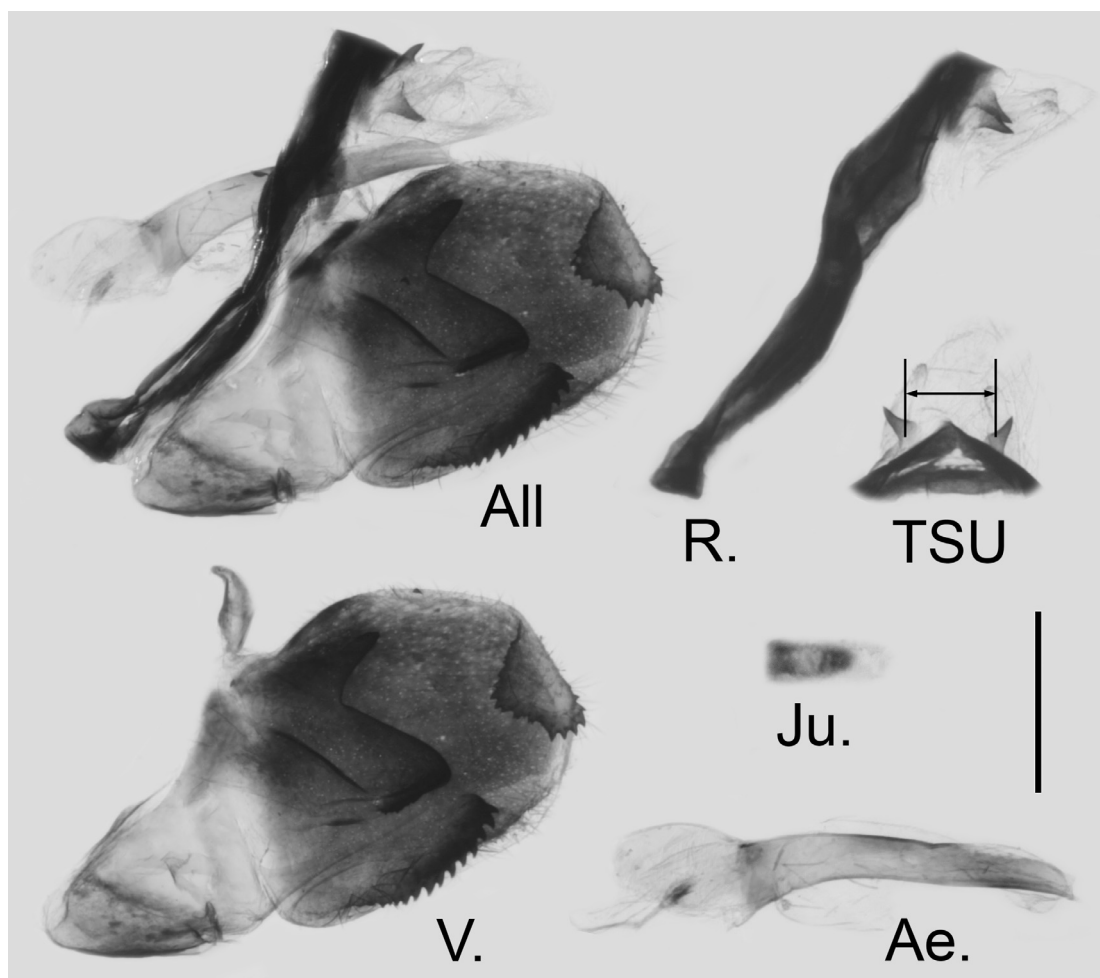


FIGURE 4. Male genitalia of *G. (P.) alebion* (Gray, [1853]) from Nanjing, Jiangsu, China; scale bar = 1.0 mm. All: genitalia as a whole, R.: lateral view of ring, TSU: dorsal view of tegumen, socii and uncus (lines and arrows indicate the distance measured), V.: right valve, Ae.: lateral view of aedeagus, Ju.: ventral view of juxta.

Diagnostic characters: Larger than *G. (P.) alebion*, forewing length: male 33.5–40.5 mm (mean = 37.6 ± 1.4 mm, $n = 83$), female 39.5–42.0 mm (mean = 40.5 ± 1.3 mm, $n = 3$). Both wings broader, ground colour dull creamy white with a slight greyish tinge; all black markings on both wings rather thick and prominent. Forewing the 1st, 2nd, 8th, 9th black bands and the terminal (10th) black band all reach tornal margin in both sexes; area between the 8th and 9th bands distinctively filled by dark scales (the extent varies among individuals but without geographical association) in male, but not in the female (only indicated near the apex); the 7th band not displaced inward in cell R_4 ; veins CuA_2 to M_2 stained with black distally. Hindwing discal band not broadened towards costa; no whitish small patch at the base of tail in cell M_3 ; tornal yellow spots much smaller and divided on both sides.

Distribution: China (W. and N.W. Yunnan, W. Sichuan, and S.E. Tibet: mostly in the upper Irrawaddy, Salween, Mekong, and Yangtze watersheds); Myanmar (N. Kachin State).

Host plants: Shao-Ji Hu observed females in ovipositing posture around bushes of *Litsea chuii* var. *likiangensis* (Lauraceae) in Yulong Xueshan, N.W. Yunnan, but no eggs were collected for rearing to confirm whether this *Litsea* is its host plant.

Male genitalia (Figure 7): In total, 20 male genitalia of specimens collected from Yunnan and Sichuan were dissected, and the general characters were consistent. Highly sclerotized. Ring slightly wavy in the upper half; saccus small but moderately sclerotized; socius toothed laterally, distance between the base of socii 0.58–0.70 mm (mean = 0.64 ± 0.05 mm, $n = 20$). Valve short, oval in general, dorsal terminal harpe long pear-shaped, edge serrate with the base separated; the medial harpe long and slightly curved, the dorsal projection bayonet-shaped with pointed or toothed tip; no tooth in the middle of the medial harpe. Aedeagus long, strongly curved ventrally. Juxta long, weakly sclerotized with hairy membrane on both sides.

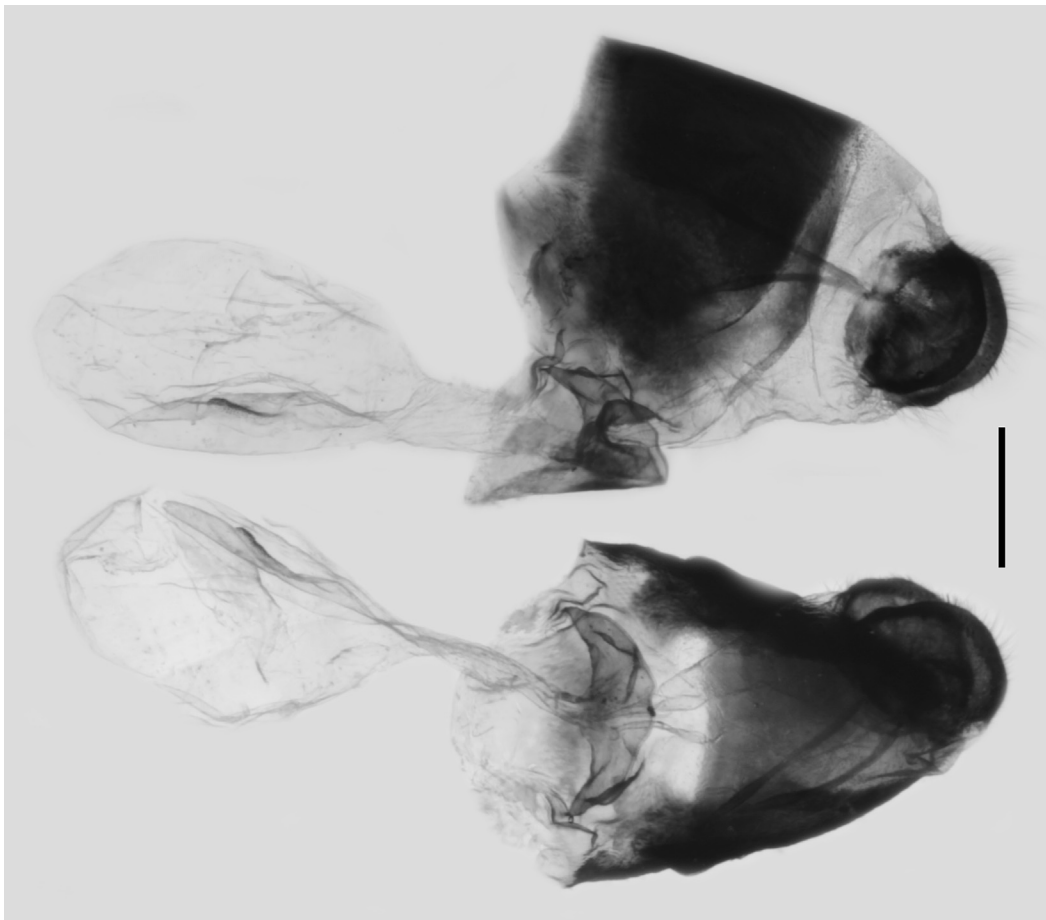


FIGURE 5. Female genitalia of *G. (P.) alebion* (Gray, [1853]) from Nanjing, Jiangsu, China; scale bar = 1.0 mm.

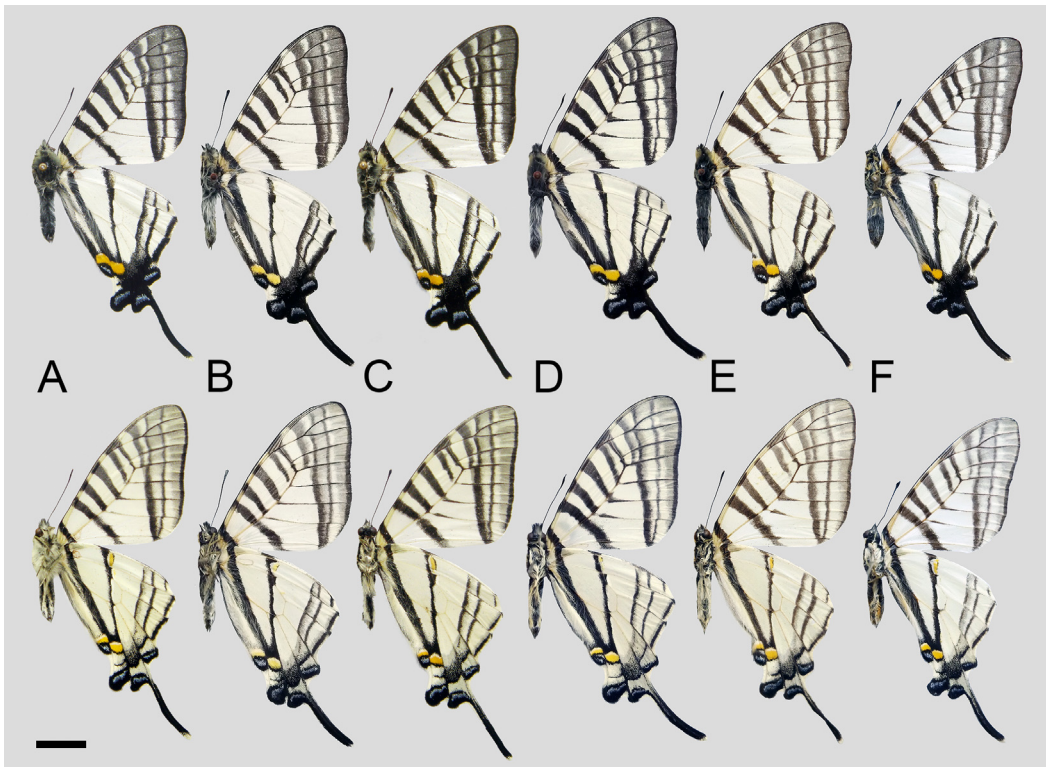


FIGURE 6. *G. (P.) parus* (Nicéville, 1900); upperside above, underside below; scale bar = 10 mm. A: ♂, Weixi, Yunnan, China; B: ♂, Zhongdian, Yunnan, China; C–D: ♂, Yulong Xueshan, Yunnan, China; E: ♀, ditto; ♂, F: Baoxing, Sichuan, China.

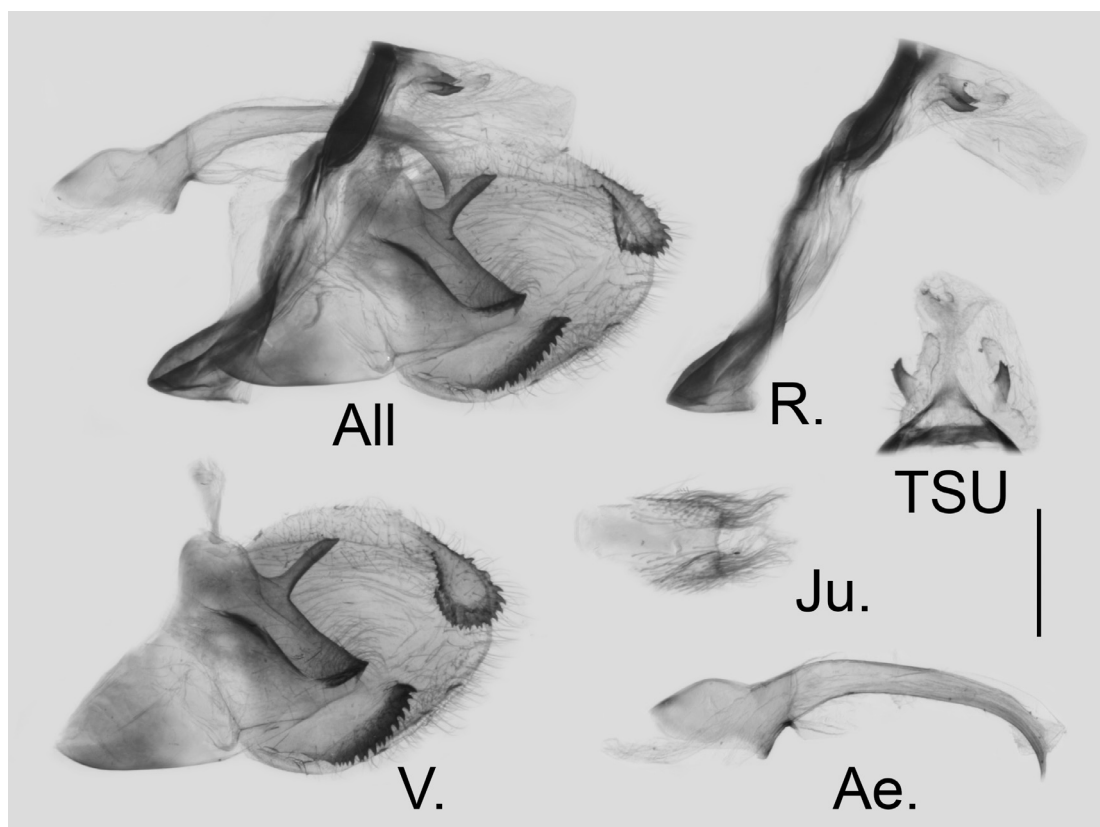


FIGURE 7. Male genitalia of *G. (P.) parus* (Nicéville, 1900) from Yulong Xueshan, Lijiang, N.W. Yunnan, China; scale bar = 1.0 mm. All: genitalia as a whole, R.: lateral view of ring, TSU: dorsal view of tegumen, socii and uncus, V.: right valve, Ae.: lateral view of aedeagus, Ju.: ventral view of juxta.

Female genitalia (Figure 8): In total, two females were available for dissection, and the characters are consistent. Lamella postvaginalis small; lamella antevaginalis broad horizontally, covered with sclerotized wrinkles; ostial lobe much less sclerotized, sac-shaped with a blunt bifurcate tip in lateral view, the posterior margin curved with slight indentations in ventral view, and the ventral surface possesses a pair of small lobes in the median portion.

***Graphium (Pazala) tamerlanus* (Oberthür, 1876) (Figure 9)**

Papilio Tamerlanus Oberthür, 1876; Ét. Ent., 2: 13, pl. II, f. 1; TL: ‘Moupin’ [Baoping, Sichuan, China].

Diagnostic characters: The largest of the three species, both wings broad, ground colour pale white; all black markings on both wings thinner. Forewing the 1st, 2nd, 8th black bands all reach tornal margin in both sexes, while the 9th black band tends to be reduced near the tornus, and the terminal (10th) black band usually only reaches or just crosses vein CuA₂; dark scales between the 8th and 9th bands only indicated near the apex; the 7th band not displaced inward in cell R₄; veins CuA₂ to M₂ only faintly stained with black distally. Hindwing discal band not broadened towards costa; no whitish small patch at the base of tail in cell M₃; tornal yellow spots much smaller and divided on both sides.

Male genitalia (Figure 10): In total, 10 male genitalia were dissected for the two known subspecies, namely ssp. *tamerlanus* and ssp. *kansuensis*, and the general characters were consistent. Highly sclerotized. Ring slightly wavy in the upper half; saccus small but moderately sclerotized; socius toothed laterally, distance between the base of socii 0.40–0.60 mm (mean = 0.49 ± 0.08 mm, *n* = 10). Valve short, oval in general, dorsal terminal harpe short, pear-shaped with both lower angles more acute, edge serrate with the base connected; the medial harpe long and slightly curved, the dorsal projection bayonet-shaped with pointed or toothed tip; no tooth in the middle of the medial harpe. Juxta weakly sclerotized with hairy membrane on both sides.

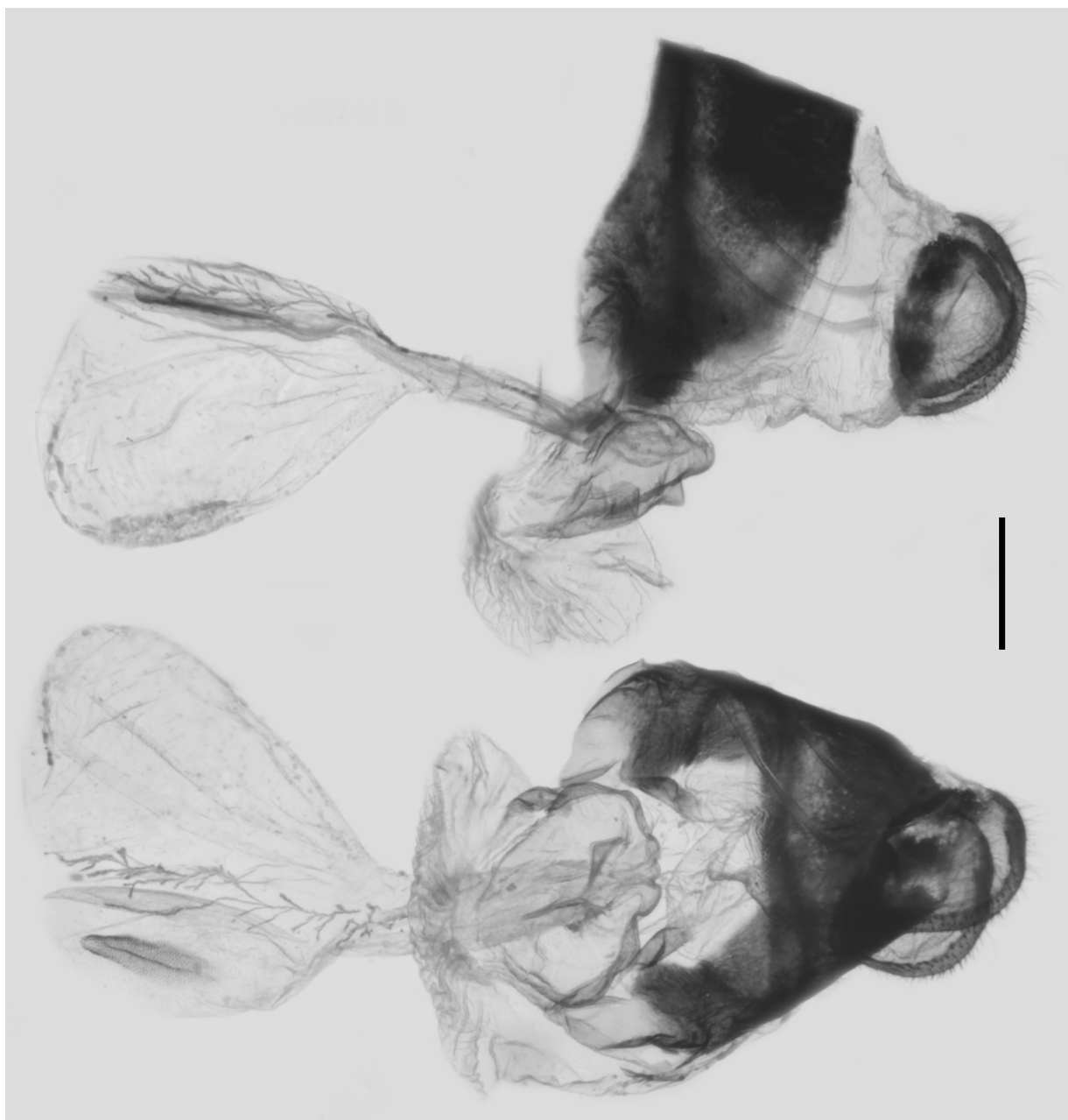


FIGURE 8. Female genitalia of *G. (P.) parus* (Nicéville, 1900) from Yulong Xueshan, Lijiang, N.W. Yunnan, China; scale bar = 1.0 mm.

Female genitalia (Figure 11): In total, two females of ssp. *tamerlanus* and a female of ssp. *kansuensis* were available for dissection, and the overall characters were consistent. Lamella postvaginalis small; lamella antevaginalis broad horizontally, covered with sclerotized wrinkles; ostial lobe heavily sclerotized, broad at the base and gradually narrowed into a triangular tip in lateral view, the posterior margin smooth in ventral view in two females of ssp. *tamerlanus*, and only very shallowly indented into “W”-shape in the only female of ssp. *kansuensis*.

***Graphium (Pazala) tamerlanus tamerlanus* (Oberthür, 1876) (Figure 9, A–C)**

Papilio Tamerlanus Oberthür, 1876; Ét. Ent., 2: 13, pl. II, f. 1; TL: ‘Moupin’ [Baoxing, Sichuan, China].

Pazala tamerlana Chou, 1994; Monographia Rhopalocerorum Sinensium: 55, 174. [unjustified emendation, attributed to Oberthür]

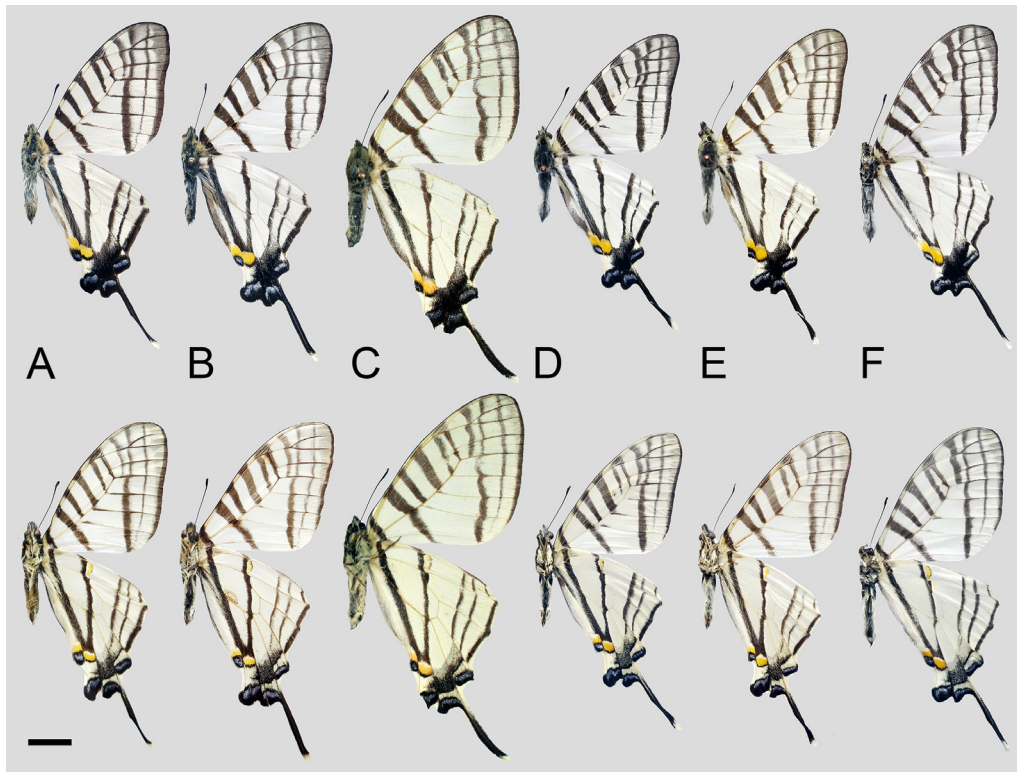


FIGURE 9. *G. (P.) tamerlanus* (Oberthür, 1876); upperside above, underside below; scale bar = 10 mm. A–C: ssp. *tamerlanus* (Oberthür, 1876), ♂(A–B), Baoxing, Sichuan, China, ♀(C), Pingwu, Sichuan, China, © Peking University; D–F: ssp. *kansuensis* (O. Bang-Haas, 1933), ♂(D–E), ♀(F), Ningshan, Shaanxi, China.

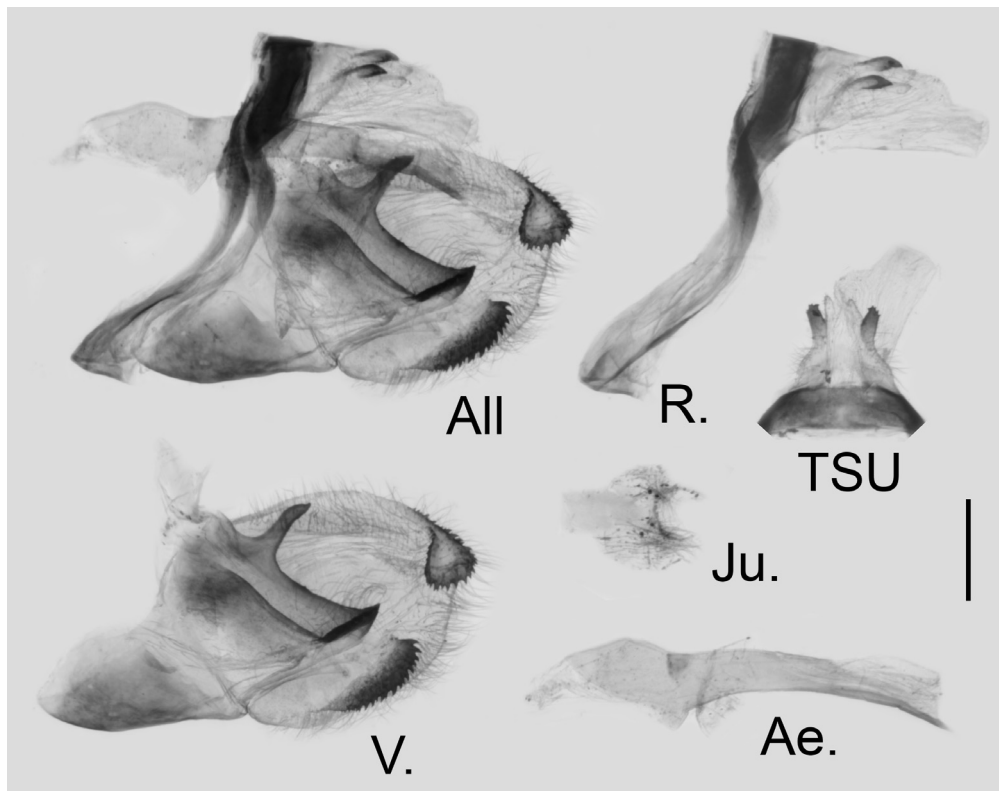


FIGURE 10. Male genitalia of *G. (P.) tamerlanus tamerlanus* (Oberthür, 1876) from Baoxing, Sichuan, China; scale bar = 1.0 mm. All: genitalia as a whole, R.: lateral view of ring, TSU: dorsal view of tegumen, socii and uncus, V.: right valve, Ae.: lateral view of aedeagus, Ju.: ventral view of juxta.

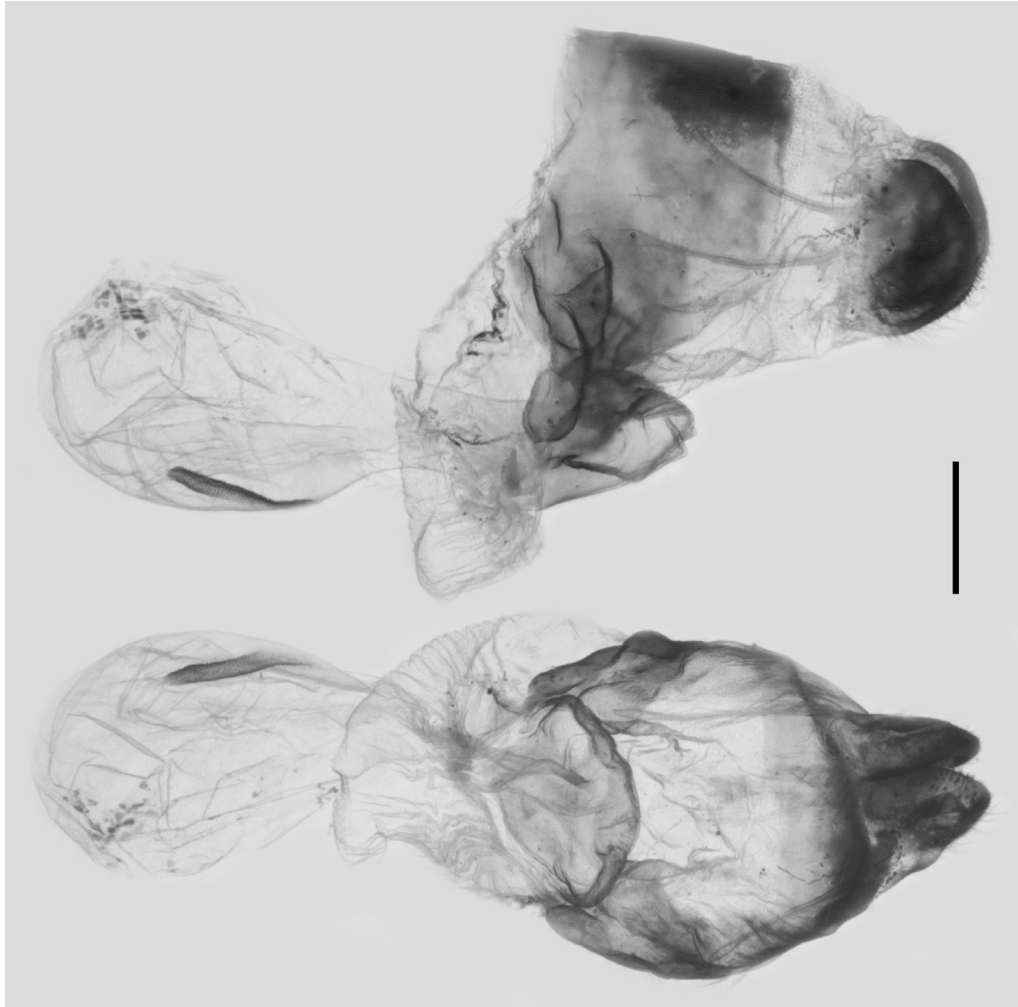


FIGURE 11. Female genitalia of *G. (P.) tamerlanus tamerlanus* (Oberthür, 1876) from Pingwu, Sichuan, China; scale bar = 1.0 mm.

Diagnostic characters: Forewing length: male 37.5–43.5 mm (mean = 40.4 ± 1.4 mm, $n = 52$), female 45.5 mm. Both wings rather broad, the 9th black band of forewing mostly reaches vein 1A in males while reduced to vein CuA_2 in females, the subterminal double black bands more separated from each other.

Distribution: The northeastern margin of the Hengduan Mountains in W. China, mainly in the medium-high altitude areas west of the Sichuan Basin.

Phenology: Specimen records indicate the flight period lasts from April to July, with those collected in June and July distinctly larger. Whether this species is univoltine or bivoltine requires further investigation.

Host plant: Unknown. Probably a plant belonging to the family Lauraceae.

***Graphium (Pazala) tamerlanus kansuensis* (O. Bang-Haas, 1933) (Figure 9, D–F)**

Cosmodesmus tamerlanus kansuensis O. Bang-Haas, 1933; Ent. Zeit, 47(11): 90; TL: ‘Kansu mer. or., Tsinglingschan, Peilingschan’ [Qinling, S.E. Gansu, China].

Graphium mathias Wang, Chen & Wang, 1990, Butt. Fauna Henan: 7, pl. 9, f. 12. [Nomen nudum, attributed to Oberthür]

Diagnostic characters: Smaller than the nominate subspecies, forewing length: male 33.5–39.0 mm (mean = 37.3 ± 1.6 mm, $n = 17$), female 39.0–40.0 mm (mean = 39.7 ± 0.6 mm, $n = 3$). Both wings narrower and slightly elongate, the 9th black band of forewing reduced even before vein CuA_2 in both sexes, the subterminal double black bands obviously close to each other.

Distribution: Confined to the Qinling Mountains in S.E. Gansu, southern Shaanxi and western Henan provinces, China.

Phenology: Specimen records indicate the flight period mainly lasts from April to June, but also as late as August (syntypes). Whether this species is univoltine or bivoltine requires further investigation.

Host plant: Unknown. Probably a plant belonging to the family Lauraceae.

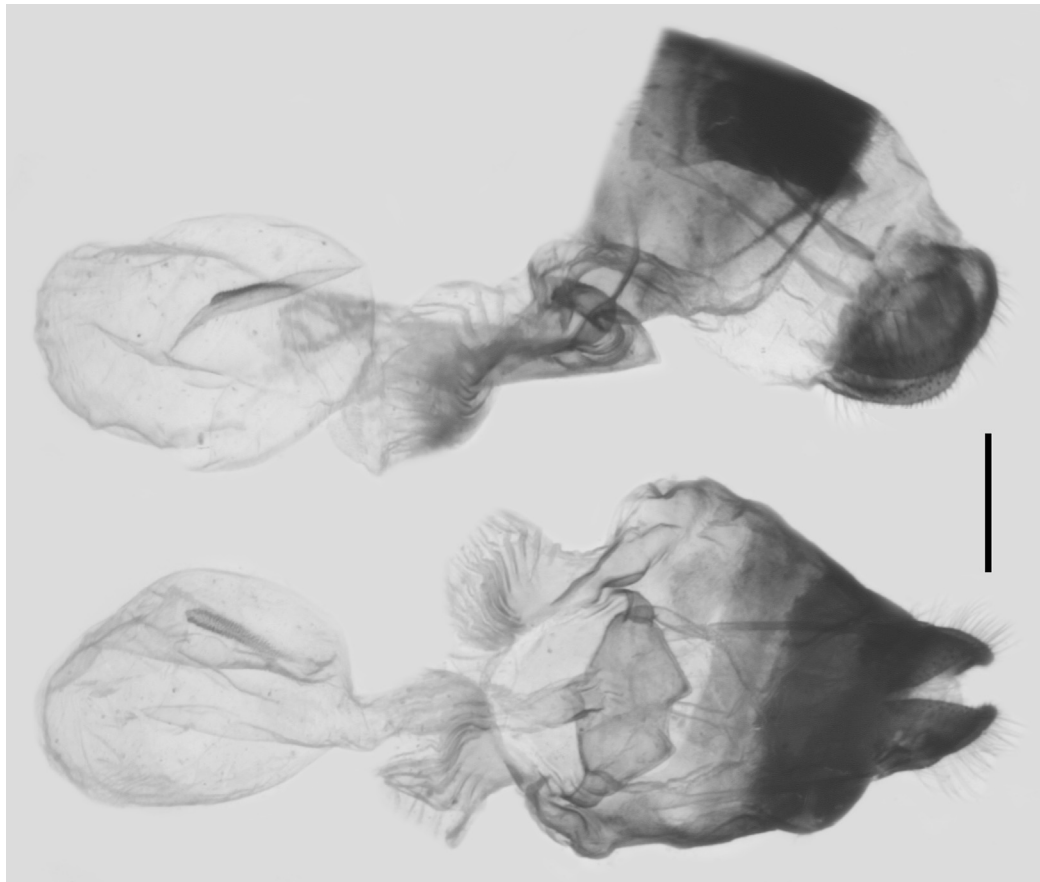


FIGURE 12. Female genitalia of *G. (P.) tamerlanus kansuensis* (O. Bang-Haas, 1933) from Ningshan, Shaanxi, China; scale bar = 1.0 mm.

Discussion

The *alebion* group is relatively old in phylogenetic position, diverging before all other species in subgenus *Pazala*. Unlike other groups that possess subspecies and cryptic taxa throughout their distribution range (Racheli & Cotton 2009; Hu *et al.* 2018; Hu *et al.* 2019), there is no taxon diversity within the *alebion* group. *G. (P.) alebion* is the only species in this group, and our analyses did not identify any new taxa. Although the taxa within the *tamerlanus* group diverged later than those of the *mandarinus*, *eurous*, and *mullah* groups, it also lacks low-altitude sister taxa compared to the *mandarinus* and *eurous* groups (Racheli & Cotton 2009; Hu *et al.* 2018; Hu *et al.* 2019), indicating slow historical radiation for this group. *G. (P.) tamerlanus* is the only species with subspecies in this study, and molecular evidence inferred that the divergence between the two subspecies separated by the Qinling Mountains is quite recent (Table 3; Figure 2). Since the Qinling Mountains arose in a significantly old geological time (Meng 2017), the authors tend to believe the split of the two subspecies might more likely be attributed to climate change in the Pleistocene as stated by Hu *et al.* (2018) rather than tectonic shifts.

Taxonomic and distribution confusions have long been coupled with each other among the three focal species of this study. Mell (1938) split *G. (P.) tamerlanus* into multiple subspecies across a very wide range in China: including ssp. *hoenei* from E. China [= *G. (P.) hoeneanus* Cotton & Hu, 2018] and Sichuan [= *G. (P.) sichuanica* Koiwaya, 1993]; ssp. *taliensis* from Dali, W. Yunnan and ssp. *parus* from Tsekou, Yunnan [both = *G. (P.) parus*]. Lee & Zhu (1992: pl. 37 & 38, f. 2) illustrated a male '*Pazala tamerlanus* (Oberthür)', which is actually a pale example of *G.*

(*P.*) *parus*; the same specimen was again illustrated in Lee (1995: 52, f. 68). Racheli & Cotton (2009) stated under the taxonomic note for *G. (P.) tamerlanus*: “In ZFNIK [sic = ZFMK], in the Höne Collection, there are typical specimens of *tamerlanus* from A-tun-tse [Mekong river north of Yanmen, N Yunnan].” However, a careful re-examination of the photographed specimens from the Höne Collection of the ZFMK showed that all the females were *G. (P.) parus* rather than *G. (P.) tamerlanus* (Figure 13). Similarly, on examination in 2006, we found that the three ‘*tamerlanus*’ drawers in the collection of BMNH also contained a mixture of *G. (P.) parus* and *G. (P.) tamerlanus*. Campbell Smith curated the BMNH specimens in 2003, labelling them ‘f. *tamerlanus*’ and ‘f. *incerta*’. He also determined a male of *G. (P.) parus* from N. Kachin State, Myanmar, as ‘*Graphium t. tamerlanus* f. *parus*’. Possibly Smith had not seen Koiwaya (1993) in which he recognised *Pazala incerta* [= *G. (P.) parus*] as a separate species to *tamerlanus*. Racheli & Cotton (2009) realised that *parus* was the senior name for the same taxon as *incertus* Bang-Haas, thus confirming the valid species name.



FIGURE 13. Female *Graphium (Pazala) parus* in the Höne Collection of the ZFMK curated as *tamerlanus*; upperside on the left, underside on the right; © Zoologisches Forschungsinstitute und Museum Alexander König (ZFMK), Bonn, Germany.

Specimens sold in the west under the name ‘*Pazala alebion*’ from Sichuan in recent years have all proven to be either *G. (P.) tamerlanus* or *G. (P.) parus*. This may partly be due to confusion in the works of D’Abrera (1982, 1990), which many collectors and commercial suppliers have used for identification purposes. In his 1982 book on Oriental butterflies, D’Abrera treated *G. (Pazala) mullah chungianus* from Taiwan as ‘*Pazala alebion chungianus* [sic]’ and in the Holarctic volume (1990) he illustrated *tamerlanus* as a subspecies of ‘*Pazala alebion*’ and pictured

a male of *Graphium (Pazala) mullah* alongside an obviously different specimen of true *alebion*, both captioned as '*P. alebion alebion*'. Possibly D'Abbrera was also confused by the Shirôzu's (1961) description of *Iphiclides alebion tayal*, which is a junior synonym of *G. (Pazala) mullah chungianus* (Murayama, 1961). Murayama originally described *chungianus* as a species in genus *Iphiclides* two months before Shirôzu published his subspecies name.

To date, all reliable records of *G. (P.) alebion* are still confined to the lower Yangtze watershed in E. China (Figure 14); no specimens of *G. (P.) alebion* have been found in C. China or westward areas approaching the two aforementioned species. Racheli & Cotton (2009) illustrated a female supposedly from Taibai Shan, Shaanxi (photo obtained by the editor, G. C. Bozano, from an unverified source). However, Prof. Yu-Fei Li (Xi'an, China) has studied butterflies of Taibai Shan for over 20 years and stated (pers. comm.) that he had never seen *G. (P.) alebion* there in his lifetime. The widely ranging distribution for this species recorded in Chou (1994) including most of China and India must comprise many misidentifications. Wu (2001) similarly includes Sichuan and even Yunnan in the distribution of *alebion*. Further surveys in C. China in late February to March are required to finally elucidate the western limit of this species.

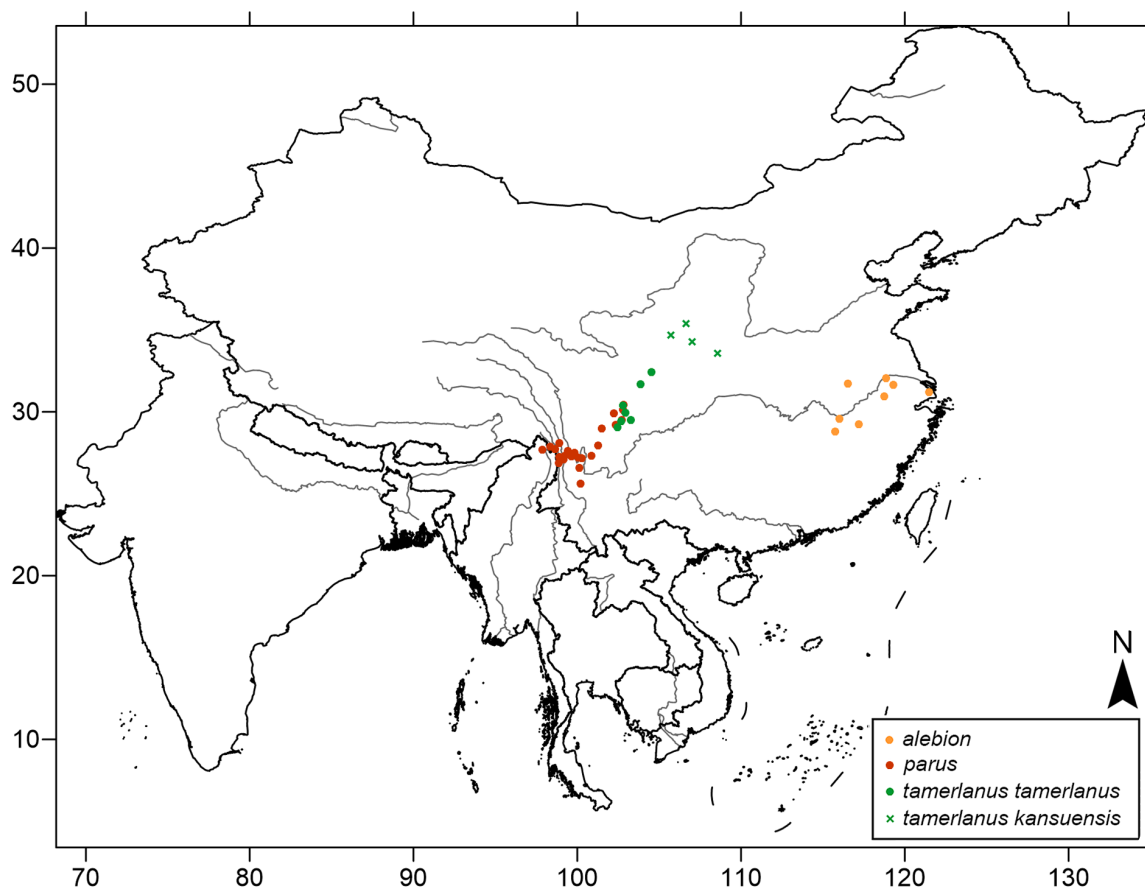


FIGURE 14. Distribution map of the *Graphium (Pazala) alebion* and *G. (P.) tamerlanus* groups as per the geographical range of Hu *et al.* (2018).

We think that such confusions were mainly caused by the similar wing pattern and male genitalic structure of the three species, especially the single, non-bifurcated hindwing discal band, which differs from all other *Pazala* species. However, the micro characters on both wings and the terminal process of male genitalia can be used to separate the three species effectively. Our study confirmed that the ostial lobes in female genitalia of the three species are totally different, demonstrating that they are three distinct species. This is also supported by the Bayesian phylogenetic tree and the estimates of divergence times showing three clades (Figure 1). Racheli & Cotton (2009) speculated a closer relationship between *G. (P.) alebion* and *G. (P.) mullah* than the *tamerlanus* group, based on the large undivided tornal yellow spots and forwardly expanded hindwing discal band. Our analysis and a previous study (Figure 1; Hu *et al.* 2018) showed that *G. (P.) mullah* was more distant than the *tamerlanus* group, which does not possess such characters. We think the two typical characters might represent the ancestral state of *G. (P.) alebion* which were lost in the course of divergence into the *tamerlanus* group and regained by *G. (P.) mullah*.

Our field survey and collection covering most altiplano and mountains of N. and N.W. Yunnan over a decade never found *G. (P.) tamerlanus*. All reliable records of *G. (P.) tamerlanus* extend from the western margin of the Sichuan Basin northeastwardly to the southwest corner of the Qinling Mountains. In comparison, the distribution range of *G. (P.) parus* occupies the entire montane area in the upper Irrawaddy, Salween, Mekong, and Yangtze watersheds in W. and N.W. Yunnan, and extends northeastwardly to the western margin of the Sichuan Basin, where *G. (P.) tamerlanus* is sympatric (Figure 14). The range of both species may be slightly wider than recorded, but based on the current data, it is unlikely that *G. (P.) tamerlanus* would reach Yunnan across the Yangtze valley.

Acknowledgements

The authors wish to thank Prof. Yu-Fei Li (Xi'an, Shaanxi, China), Wei-Wei Mao (Shanghai, China), Jia-Qi Wang (Shanghai, China) and Zhuo-Heng Jiang (Nanjing, China) for providing samples, specimen biometric data, and distribution information; Ping Hu (Peking University, Beijing, China) and Zhen-Li Shen (Kunming, China) for assistance in collecting specimens from W. Yunnan; and Jian-Qing Zhu (Shanghai Zoological Park, Shanghai, China) for allowing us using the photos of *G. (P.) alebion*. Additionally, the authors wish to thank the Trustees of the Natural History Museum (BMNH), London, UK, Campbell Smith[†], Phillip Ackery, and Blanca Huertas for assistance in accessing the BMNH collection. Thanks also are given to Dieter Stüning and Zoologisches Forschungsinstitute und Museum Alexander Koenig (ZFMK), Bonn, Germany, for assistance while studying the Höne Collection housed there and Marianne Espeland for permission to reproduce photographs of specimens in the ZFMK collection. Gerardo Lamas (Universidad Nacional Mayor de San Marcos, Lima, Peru) and Dick Vane-Wright (University of Kent, UK) are thanked for advice on nomenclatorial issues. This study was funded by the National Key R&D Programme of China (2017YFC0505200), the NSFC Programme of China (41761011) and the Biodiversity Conservation Programme of the Ministry of Ecology and Environment, China (China-BON Butterflies) (SDZXWJZ01013).

References

- Ayres, D.L., Darling, A., Zwickl, D.J., Beerli, P., Holder, M.T., Lewis, P.O., Huelsenbeck, J.P., Ronquist, F., Swofford, D.L., Cummings, M.P., Rambaut, A. & Suchard, M.A. (2012) BEAGLE: an application programming interface and high-performance computing library for statistical phylogenetics. *Systematic Biology*, 61, 170–173.
<https://doi.org/10.1093/sysbio/syr100>
- Bang-Haas, O. (1927) *Horae Macrolepidopterologicae Regionis Palaearcticae. Vol. 1.* Verlag O. Staudinger & Bang-Haas, Dresden-Blasewitz, 128 pp., 1 taf. [in German]
- Bang-Haas, O. (1933) Neubeschreibung und berichtigungen der Palaearktischen Macrolepidopterenfauna. V. *Entomologische Zeitschrift*, 47, 90–92. [in German]
- Bertheau, C., Schuler, H., Krumböck, S., Arthofer, W. & Stauffer, C. (2011) Hit or miss in phylogenetic analyses: the case of the cryptic NUMTs. *Molecular Ecology Resources*, 11, 1056–1059.
<https://doi.org/10.1111/j.1755-0998.2011.03050.x>
- Butler, A.G. (1881) Description of new species of Lepidoptera in the collection of the British Museum. *The Annals and Magazine of Natural History*, Series 5, 7 (37), 31–37, pl. IV.
<https://doi.org/10.1080/00222938109459469>
- Chou, I. (1994) *Monographia Rhopalocerorum Sinensium*. Henan Science and Technology Publishing House, Zhengzhou, 9 + 852 pp. [in Chinese with English descriptions for new taxa]
- Condamine, F.L., Sperling, F.A.H., Wahlberg, N., Rasplus, J.-Y. & Kergoat, G.J. (2012) What causes latitudinal gradients in species diversity? Evolutionary processes and ecological constraints on swallowtail biodiversity. *Ecology Letters*, 15, 267–277.
<https://doi.org/10.1111/j.1461-0248.2011.01737.x>
- D'Abrera, B. (1982) *Butterflies of the Oriental Region. Part I. Papilionidae, Pieridae & Danaidae*. Hill House, Victoria, xxi + 244 pp.
- D'Abrera, B. (1990) *Butterflies of the Holarctic Region. Part I. Papilionidae, Pieridae, Danaidae & Satyridae (Partim)*. Hill House, Victoria, 185 pp.
- Folmer, O., Black, M.B., Hoch, W., Lutz, R.A. & Vrijehock, R.C. (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3, 294–299.
- Gray, G.R. (1852) *Catalogue of Lepidopterous Insects in the Collection of the British Museum. Part I. Papilionidae*. Taylor and Francis, London, 84 pp. XIII pls.

- Hall, T.A. (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nuclear Acids Symposium Series*, 41, 95–98.
- Hu, S.J., Cotton, A.M., Condamine, F.L., Duan, K., Wang, R.J., Hsu, Y.F., Zhang, X. & Cao, J. (2018) Revision of *Pazala* Moore, 1888: the *Graphium* (*Pazala*) *mandarinus* (Oberthür, 1879) group, with treatments of known taxa and descriptions of new species and new subspecies (Lepidoptera: Papilionidae). *Zootaxa*, 4441 (3), 401–446. <https://doi.org/10.11646/zootaxa.4441.3.1>
- Hu, S.J., Condamine, F.L., Monastyrskii, A.L. & Cotton, A.M. (2019) A new species of the *Graphium* (*Pazala*) *mandarinus* group from Central Vietnam (Lepidoptera: Papilionidae). *Zootaxa*, 4554 (1), 286–300. <https://doi.org/10.11646/zootaxa.4554.1.10>
- Huelsenbeck, J.P., Larget, B. & Alfaro, M.E. (2004) Bayesian phylogenetic model selection using reversible jump Markov Chain Monte Carlo. *Molecular Biology and Evolution*, 21, 1123–1133. <https://doi.org/10.1093/molbev/msh123>
- Koiwaya, S. (1993) Description of three new genera, eleven new species and seven new subspecies of butterflies from China. *Studies of Chinese Butterflies*, 2, 43–111, pls. 9–27. [in Japanese with English descriptions]
- Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T. & Calcott, B. (2017) PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution*, 34, 772–773. <https://doi.org/10.1093/molbev/msw260>
- Lee, C.L. (1995) *The Butterflies of Yunnan*. Chinese Forestry Press, Beijing, 152 pp. [in Chinese]
- Lee, C.L. & Zhu, B.Y. (1992) *Atlas of Chinese Butterflies*. Far East Press, Shanghai, 79 pp., 152 pls. [in Chinese]
- Miller, M.A., Schwartz, T., Pickett, B.E., He, S., Klem, E.B., Scheuermann, R.H., Passarotti, M., Kaufman, S. & O’Leary, M.A. (2015) A RESTful API for access to phylogenetic tools via the CIPRES science gateway. *Evolutionary Bioinformatics Online*, 11, 43–48. <https://doi.org/10.4137/EBO.S21501>
- Mell, R. (1938) Beiträge zur Fauna sinica. XVII. Inventur und ökologisches Material zur einer Biologie der südchinesische Lepidopteren. *Deutsche Entomologische Zeitschrift*, 1938, 197–345. [in German] <https://doi.org/10.1002/mmnd.48019380204>
- Meng, Q.R. (2017) Origin of the Qinling Mountains. *Scientia Sinica Terrae*, 47, 412–420. [in Chinese] <https://doi.org/10.1360/N072016-00422>
- Meyer, C.P. & Paulay, G. (2005) DNA barcoding: error rates based on comprehensive sampling. *PLoS Biology*, 3 (12), e422. <https://doi.org/10.1371/journal.pbio.0030422>
- Moore, F. (1888) Additional Species Family Papilionidae. In: *Hewitson & Moore (1879–1888), Description of New Indian Lepidopterous Insects from the Collection of the Late Mr. W.S. Atkinson, M.A., F.L.S., & c., Director of the Public Instruction, Bengal. Rhopalocera. Part III.* Asiatic Society of Bengal, Calcutta, pp. 283–285.
- Murayama, S (1961) Eine neue Papilioniden Formosas. *Insect Science*, 12, 7–8.
- Mutanen, M., Kivelä, S.M., Vos, R.A., Doorenweerd, C., Ratnasingham, S., Hausmann, A., Huemer, P., Dincă, V., van Nieukerken, E.J., Lopez-Vaamonde, C., Vila, R., Aarvik, L., Decaëns, T., Efetov, K.A., Hebert, P.D.N., Johnsen, A., Karsholt O., Pentinsaari, M., Rougerie, R., Segerer, A., Tarmann, G., Zahir, R. & Godfray, H.C.J. (2016) Species-level para- and polyphyly in DNA barcode gene trees: strong operational bias in European Lepidoptera. *Systematic Biology*, 65, 1024–1040. <https://doi.org/10.1093/sysbio/syw044>
- Nicéville, L.de. (1900) On new and little-known Lepidoptera from the Oriental Region. *Journal of Bombay Natural History Society*, 13, 157–176, pls. CC–EE.
- O’Neill, S.L., Giordano, R., Colbert, A.M.E., Karr, T.L. & Robertson, H.M. (1992) 16S rRNA phylogenetic analysis of the bacterial endosymbionts associated with cytoplasmic incompatibility in insects. *Proceedings of the National Academy of Sciences of the United States of America*, 89, 2699–2702. <https://doi.org/10.1073/pnas.89.7.2699>
- Oberthür, C. (1876) Lépidoptères nouveaux de la Chine. *Études d’Entomologie*, 2, 13–34, pls. I–IV. [in French]
- Racheli, T. & Cotton, A.M. (2009) *Guide to the Butterflies of the Palearctic Region. Papilionidae. Part I.* Omnes Artes, Milano, 70 pp.
- Rambaut, A., Drummond, A.J., Xie, D., Baele, G. & Suchard, M.A. (2018) Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology*, 67 (5), 901–904. <https://doi.org/10.1093/sysbio/syy032>
- Rehm, P., Borner, J., Meusemann, K., von Reumont, B.M., Simon, S., Hadrys, H., Misof, B. & Burmester, T. (2011) Dating the arthropod tree based on large-scale transcriptome data. *Molecular Phylogenetics and Evolution*, 61, 880–887. <https://doi.org/10.1016/j.ympev.2011.09.003>
- Ronquist, F., Teslenko, M., Van Der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Shirôzu, T. (1961) A Papilionid Butterfly new to the Fauna of Formosa. *Tyô to Ga*, 12, 23–29.
- Song, H., Buhay, J.E., Whiting, M.F. & Crandall, K.A. (2008) Many species in one: DNA barcoding overestimates the number

- of species when nuclear mitochondrial pseudogenes are coamplified. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 13486–13491.
<https://doi.org/10.1073/pnas.0803076105>
- Tamura, K., Stecher, G., Peterson, D., Filipski, A. & Kumar, S. (2013) MEGA6: Molecular evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution*, 30, 2725–2729.
<https://doi.org/10.1093/molbev/mst197>
- Thompson, J.D., Higgins, D.G. & Gibson, T.J. (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research*, 22, 4673–4680.
<https://doi.org/10.1093/nar/22.22.4673>
- Thorne, J.L. & Kishino, H. (2002) Divergence time and evolutionary rate estimation with multilocus data. *Systematic Biology*, 51, 689–702.
<https://doi.org/10.1080/10635150290102456>
- Thorne, J.L., Kishino, H. & Painter, I.S. (1998) Estimating the rate of evolution of the rate of molecular evolution. *Molecular Biology and Evolution*, 15, 1647–1657.
<https://doi.org/10.1093/oxfordjournals.molbev.a025892>
- Wang, Z.G., Chen, L.H. & Wang, Z.Y. (1990) *Butterfly Fauna of Henan*. Henan Science & Technology Publishing House, Zhengzhou, 69 pp., 45 pls.
- Wu, C.S. (2001) *Fauna Sinica Insecta. Vol. 25. Lepidoptera Papilionidae*. Science Press, Beijing, 367 pp., 8 pls.
- Zhang, H.H., Duan, K. & Hu, S.J. (2018) On the immature stages of *Graphium (Pazala) confucius* Hu, Duan & Cotton, 2018 observed in Kunming, Yunnan, China. *Butterflies*, 79, 19–25.

APPENDIX 1. List of *Graphium (Pazala) alebion* and *G. (P.) tamerlanus* groups specimens examined, with different labels in museum specimens separated with a ‘/’.

Names of depositories are given in alphabetical order, with institutions listed after private collections, and are abbreviated as follows: AMC: collection of Adam M. Cotton (Chiang Mai, Thailand); HHZ: collection of Hui-Hong Zhang (Kunming, China); HSC: collection of Harrow School (Harrow, United Kingdom); JQW: collection of Jia-Qi Wang (Shanghai, China); SJH: collection of Shao-Ji Hu (Kunming, China); TR: collection of Tommaso Racheli (Rome, Italy); WWM: collection of Wei-Wei Mao (Shanghai, China); YFL: collection of Yu-Fei Li (Xi’an, China); BMNH: collections of the Natural History Museum (London, United Kingdom); MNHU: collection of Museum für Naturkunde der Humboldt-Universität (Berlin, Germany); NZC: collection of National Zoological Collection, Zoological Survey of India (Kolkata, India); PKU: Peking University (Beijing, China); ZFMK: collection of Zoologisches Forschungsinstitute und Museum Alexander Koenig (Bonn, Germany).

Graphium (Pazala) alebion (Gray, [1853])

CHINA: 1♂**SYNTYPE**, Shanghai, N. China, Fortune Coll. 52–28/**LECTOTYPE** *Papilio alebion* G. R. Gray C. R. Smith det. 2003/BMNH(E) # 149382, [BMNH]; 1♂**HOLOTYPE** [of *Papilio mariesii* Butler, 1881], Kiukiang 80 · 25./**HOLOTYPE** *Papilio mariesii* Butler C. R. Smith det. 2003/BMNH(E) # 149383, [BMNH]; 1♂China, Fukien. Kiukiang./Coll.Moore. BM.1903—361./BMNH(E) # 147067, [BMNH]; 1♂, Hewitson coll., 79.69, *Papilio Alebion*./BMNH(E) # 147887, [BMNH]; 1♂, Berg Pao-hwa, b. Lungtan, b.Nanking, China Juni/Rothschild Bequest B.M.1939-1./BMNH(E) # 145650, [BMNH]; 1♂, Berg Pao-hwa, b. Lungtan, b.Nanking, China Juni/Rothschild Bequest B.M.1939-1./396./BMNH(E) # 145651, [BMNH]; 1♂, China/Rothschild Bequest B.M.1939-1./BMNH (E) # 220142, [BMNH]; 1♀, Berg Paoschan, b.Nanking, China sept.or. April/50 .29/671./Levick Bequest 1941-83/BMNH(E) # 147067, [BMNH]; 1♂, Hoengshan, Prov. Hunan, 3.4. 1933. Höne [ZFMK]; 1♂, Hoengshan, Prov. Hunan, 4.4. 1933. Höne [ZFMK]; 1♀, Hoengshan, Prov. Hunan, 7.4. 1933. Höne [ZFMK]; 2♂♂, Lungtan bei Nanking, Prov. Kiangsu, 10.4. 1933. H. Höne [ZFMK]; 1♀, Ost Tien-mu-shan, Prov. Chekiang, 18.4. 1931. Höne [ZFMK]; 1♂, West Tien-mu-shan, Prov. Chekiang, 2.4. 1932. H. Höne [ZFMK]; 1♂, West-Tien-Mu-Shan (400m), Provinz Chekiang(China), Mitte April 1936. H. Höne [ZFMK]; 2♂♂, Baohua Shan, E. Nanjing, Jiangsu, 2006-IV-26, J. Q. Wang leg. [JQW]; 1♂, Baohua Shan, E. Nanjing, Jiangsu, 2007-III-22, local catcher leg. [AMC]; 1♂, Baohua Shan (200 m), E. Nanjing, Jiangsu, 2012-IV-6, Zhu leg. [YFL]; 1♀, Meiren’ao, Sijing Shan, Nanjing, Jiangsu, 2018-III-31, J. Q. Wang leg. [JQW]; 1♀, South slope of Baohua Shan, Jurong, Jiangsu, 2018-III-31, J. Q. Wang leg. [SJH]; 2♀♀, Heng Shan, Nanjing, Jiangsu, 2019-IV-7, J. Q. Wang leg. [JQW].

***Graphium (Pazala) parus* (de Nicéville, 1900)**

CHINA: 1♂**HOLOTYPE**, Tse Kou R. P. Dubernard 1895/W. China/[handwritten] *Papilio parus*, de Nicéville. ♂. TYPE./23234 H9/TYPE [NZC]; 1♂, Thibet, Tsekou R.P.Dubernard/Ex Oberthür Coll. Brit.Mus.1927—3/BMNH(E) # 147535 [BMNH]; 1♂, Tsekou P.Dubernard 1903/Ex Oberthür Coll. Brit.Mus.1927—3/BMNH(E) # 147519 [BMNH]; 1♂, Tsékou 1900 R.P.J.Dubernard/Ex Oberthür Coll. Brit.Mus.1927—3/BMNH (E) # 220147 [BMNH]; 1♂, China mer occ, Prov. Yünnan occ, Weihsi, Mekong Fluss, Juli 2500 m/Rothschild Bequest B.M.1939-1./BMNH(E) # 145648 [BMNH]; 1♂, Ta-Chien-Lu, 8300 ft., Pratt coll, May & June 1890/Rothschild Bequest B.M.1939-1./BMNH (E) # 220237 [BMNH]; 1♂, Tà-tsien-Loû, Chasseurs Indigènes 1893/Ex Oberthür Coll. Brit.Mus.1927—3/*Graphium (Pazala) t. tamerlanus* Ob. 'parus' de N. form, det CR Smith 2003/BMNH(E) # 145968 [BMNH]; 1♂, Chasseurs Indigènes de Tà-tsien-loû. Récolte de 1910/Ex Oberthür Coll. Brit.Mus.1927—3/BMNH(E) # 145740 [BMNH]; 1♂, Wa-ssu-Kow, 5000 ft., Native coll., July 1890/Rothschild Bequest B.M.1939-1./BMNH (E) # 220146 [BMNH]; 1♂, Batang.(Tibet). Im Tal des Yangtze(ca. 2800m) 17.5. 1936 H.Höne [ZFMK]; 1♂, Batang(Tibet) Talsohle ca. 2800m 10.5. 1937 Höne [ZFMK]; 1♂, Li-kiang ca.2000m Prov. Nord-Yuennan. 12.5. 1935.H.Höne [ZFMK]; 1♂, Li-kiang.(China). Provinz Nord-Yuennan. 14.5. 1935.H.Höne [ZFMK]; 1♂, A-tun-tse(N. Yünnan) Talsohle ca. 3000m 27.5. 1937.H.Höne [ZFMK]; 1♂, Weihsi [ZFMK]; 1♀, A-tun-tse (N. Yünnan) Talsohle ca. 3000m 23.5. 1936.H.Höne [ZFMK]; 1♀, A-tun-tse (Nord-Yünnan) Talsohle ca. 3000m 27.5. 1937.H.Höne [ZFMK]; 1♂, Yunnan, Jonten [= Zhongdian] 2003-VI, Ng Y-M. leg. [TR]; 1♂, Tali, Haut Yunnan [TR]; 6♂♂, Wushi He, Hanyuan, Sichuan, 2005-VII-5-20, local catcher leg. [AMC]; 2♂♂, Kangding, Sichuan, 2006-VII, local catcher leg. [AMC]; 1♂, Ya'an, Sichuan, 2006-VII, local catcher leg. [AMC]; 4♂♂, Ya'an, Sichuan, 2007-IV, local catcher leg. [AMC]; 32♂♂, Ya'an, Sichuan, 2008-IV, local catcher leg. [AMC]; 1♂, Luzhou, Sichuan, 2008-VII, local catcher leg. [AMC]; 1♂, Dulongjiang, Gongshan, Yunnan, 2009-V-20, local catcher leg. [AMC]; 1♂, Lushan, Sichuan, 2008-IV, local catcher leg. [AMC]; 10♂♂, Lushan, Ya'an, Sichuan, 2012-IV, local catcher leg. [SJH]; 1♂, Xinshang (2,640 m), Yulong Xueshan, Lijiang, Yunnan, 2015-IV-26, J. Zhao leg. [SJH]; 2♂♂, Pantiang (2,800 m), Weixi, Yunnan, 2015-IV-29, S. J. Hu leg. [SJH]; 1♂, Tacheng (1,900 m), Weixi, Yunnan, 2015-IV-29, S. J. Hu leg. [SJH]; 1♀, Lushan, Sichuan, 2015-VII-15, local catcher leg. [HHZ]; 9♂♂, Shimian (2,400 m), Sichuan, 2017-IV-20–30, C. J. Dai leg. [JQW]; 2♂♂, Hanyuan (1,700 m), Sichuan, 2017-V-5, J. Q. Wang leg. [JQW]; 1♀, Sanchahe (3,000 m), Yulong Xueshan, Lijiang, Yunnan, 2018-V-26, S. J. Hu leg. [SJH]; 1♀, Ganhaizi (3,300 m), Yulong Xueshan, Lijiang, Yunnan, 2018-VI-21, S. J. Hu leg. [SJH]; 11♂♂, Sanchahe (3,000 m), Yulong Xueshan, Lijiang, Yunnan, 2019-IV-26–27, S. J. Hu & Z. B. Xu leg. [SJH]; 1♂, Nixi (3,000 m), Zhongdian, Yunnan, 2019-VI, Y. Yang leg. [SJH].

MYANMAR: 1♂, N. Burma: Adung Valley. 8,000 ft. 12-V-1931 Lord Cranbrook. B.M.1932-196/*Graphium (Pazala) t. tamerlanus* Ob. 'parus' de N. form, det CR Smith 2003/BMNH(E) # 146767, [BMNH].

***Graphium (Pazala) tamerlanus tamerlanus* (Oberthür, 1876)**

CHINA: 1♂**SYNTYPE**, Chine R. P. Armand David Moupin/[handwritten] *Papilio tamerlanus* Ob' type. pris à Moupin par l'abbé Armand David. (Etud. entomol. Ob.2 no1)/Typicum Specimen/Levick Bequest 1941-83/**SYNTYPE** *Papilio Tamerlanus* Oberthür C.R. Smith det. 2003/BMNH(E) # 149380, [BMNH]; 1♂**SYNTYPE**, Chine R. P. Armand David/ExTypicalibus Speciminibus/Levick Bequest 1941-83/**SYNTYPE** *Papilio Tamerlanus* Oberthür C.R. Smith det. 2003/BMNH(E) # 146993, [BMNH]; 1♂, Mou-Pin 1898 Chasseurs indigènes 1893/Ex Oberthür Coll. Brit.Mus.1927—3/BMNH (E) # 220144 [BMNH]; 1♀, Wa-Shan, 6000 ft. A. E. Pratt coll. June 1889./Leech Coll. 1901—173. *Papilio tamerlanus*.g/BMNH (E) # 220236 [BMNH]; 1♂, Emei Shan, Sichuan, 1997-VII-15, local catcher leg. [AMC]; 4♂♂, Qilaishan [= Qionglai Shan], Sichuan, 2000-IV, local catcher leg. [AMC]; 4♂♂, Baoxing, Sichuan, 2001-V-5, E. T. Ye leg. [SJH]; 1♂, Daba Shan, Sichuan, 2003-VII, local catcher leg. [AMC]; 1♂, Rou Bi Gou, Baoxing, Sichuan, 2005-IV-23, Ming Yue leg. [AMC]; 2♂♂, ditto, 2005-V-15–16, Ming Yue leg. [AMC]; 2♂♂, ditto, 2006-V-18–19, Ming Yue leg. [AMC]; 1♂, ditto, 2006-VI-16, Ming Yue leg. [AMC]; 4♂♂, 1♀, Lushan, Sichuan, 2005-VI, local catcher leg. [AMC]; 21♂♂, ditto, 2006-IV-15–20, local catcher leg. [AMC]; 9♂♂, Wushi He, Hanyuan, Sichuan, 2005-VII-5–20, local catcher leg. [AMC]; 1♂, Baoxing, Sichuan, 2010-VI-15, local catcher leg. [HHZ]; 1♀, Laohegou (1,610 m), Pingwu, Sichuan, 2013-IV-11–20, C. Fan *et al.* leg. [PKU]; 4♂♂, Laohegou (1,690–2,010 m), Pingwu, Sichuan, 2013-V-1–10, C. Fan *et al.* leg. [PKU]; 1♀, Laohegou (1,600 m), Pingwu, Sichuan, 2013-VI-1–10, C. Fan *et al.* leg. [PKU]; 1♂, Lushan, Sichuan, 2015-VI-20, local catcher leg.

[HHZ]; 1♂, ditto, 2015-VII-15, local catcher leg. [HHZ]; 1♂, Shimian (2,400 m), Sichuan, 2017-IV-20–30, C. J. Dai leg. [JQW].

***Graphium (Pazala) tamerlanus kansuensis* (O. Bang-Haas, 1933)**

CHINA: 1♂SYNTYPE, Liojiang Prov. Kansu Tsin-ling-schan montes occ. August 1000 m./Type O. B.-Haas [MNHU]; 1♂SYNTYPE, Kansu mer. Peiling shan Taupingfluß 3200 m. Juni/Type O. B.-Haas/[handwritten] P Cosmod tamerlanus v Kansuensis O.B.H. [MNHU]; 1♂, Tapaishan im Tsinling Sued-Shensi.Ca.1700m. 11.5. 1936. H.Höne [ZFMK]; 1♂, Tapaishan im Tsinling Sued-Shensi.Ca.1700m. 17.5. 1936.H.Höne [ZFMK]; 1♂, Tapaishan im Tsinling Sued-Shensi.Ca.1700m. 22.5. 1936.H.Höne [ZFMK]; 1♀, Tapaishan im Tsinling Sued-Shensi. Ca.1700m. 17.5. 1936.H.Höne [ZFMK]; 1♂, Kansu mer., Lih sien, Tauping Fluss, 2800 m., Juni/[handwritten] alebion subspecies/64. [HSC]; 1♀, Shibianyu, Chang'an, Shaanxi, 1999-V-2, Y. F. Li leg. [YFL]; 1♂, Fenghuang Shan, Hanyin, Shaanxi, 2000-V-1, Y. F. Li leg. [YFL]; 1♀, Qinling Station, Fengxian, Shaanxi, 2001-V-6, Y. F. Li leg. [YFL]; 3♂♂, Xiaonanhai, Nanzheng, Shaanxi, 2002-IV-20, Y. F. Li leg. [YFL]; 1♂, Xunyang Ba (1,500 m), Ningshan, Shaanxi, 2010-V-23, Y. F. Li leg. [YFL]; 1♂, Dayu (1,900 m), Chang'an, Shaanxi, 2010-V-29, Y. F. Li leg. [YFL]; 1♂, Xunyang Ba (1,600 m), Ningshan, Shaanxi, 2011-V-24, Y. F. Li leg. [YFL]; 1♂, Huangguan, Ningshan, Shaanxi, 2012-V-21, Y. F. Li leg. [YFL]; 1♂, Xiaohanhai (1,500 m), Nanzheng, Shaanxi, 2012-VI-9, Y. F. Li leg. [YFL]; 3♂♂, Shangba He (1,200 m), Ningshan, Shaanxi, 2013-IV-12, W. W. Mao leg. [WWM & SJH]; 2♂♂, Xunyang Ba (1,300 m), Ningshan, Shaanxi, 2013-IV-16, W. W. Mao leg. [WWM & SJH]; 1♂, Shangba He (1,300 m), Ningshan, Shaanxi, 2013-IV-20, Y. F. Li leg. [HHZ]; 1♂, Yindong Xia (1,000 m), Baoji, Shaanxi, 2015-IV-22, W. W. Mao leg. [SJH]; 1♂, 1♀, Yuehe Ping (1,500 m), Ningshan, Shaanxi, 2015-V-23, W. W. Mao leg. [SJH].