

RESEARCH PAPER

Revision of the taxonomic status of *Amathuxidia morishitai* from Hainan, China (Lepidoptera: Nymphalidae)

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Abstract. Based on the external characters, genital structures, distribution, and intermediate individuals from contact zones, the endemic species *Amathuxidia morishitai* Chou & Gu, 1994 from Hainan, China is treated as conspecific with *A. amythaon* (Doubleday, 1847) and is downranked to a subspecies of the latter, i.e., *Amathuxidia amythaon morishitai* stat. nov. Meanwhile, two subspecies groups of *A. amythaon* are recognized by morphological and genetic evidence, termed *amythaon*-group (*A. a. amythaon* + *A. a. dilucida* (Honrath, 1884)) and *annamensis*-group (*A. a. morishitai* + *A. a. annamensis* Talbot, 1932) with the latter group showing a deeper divergence than normal on a subspecific level genetically.

Key words. Lepidoptera, Nymphalidae, Satyrinae, Amathusiini, endemic, genitalia, molecular phylogeny, sex brands, China

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Introduction

The Oriental genus *Amathuxidia* Staudinger, [1887] is a large-sized Amathusiini well-known for the magnificent blue glory of its males (STAUDINGER 1884–1888). More than a century after its establishment, only two species of this genus were known, viz., *A. amythaon* (Doubleday, 1847) and *A. plateni* (Staudinger, [1887]), until the third one was erected in a monography edited by CHOU (1994) based on a male from Hainan, China, namely *A. morishitai* Chou & Gu, 1994 (DOUBLEDAY 1847, FRUHSTORFER 1911).

However, *A. morishitai* was poorly described and granted a specific status without a convincing diagnosis. In the original paper, instead of comparing it to its congeners, Chou & Gu (CHOU 1994), for unclear reasons, compared *A. morishitai* to *Thaumantis odana* (Godart, [1824]), a species from a different genus, leaving the diagnostic characteristics of *A. morishitai* undefined

(LATREILLE & GODART 1824). Subsequently, based on a specimen figured in GU & CHEN (1997), LANG (2012) suggested that this insular taxon can be separated from *A. amythaon* by the shape of the blue band on the forewing upperside. Nonetheless, the species-level of *A. morishitai* is still debatable with most subsequent authors following the original opinion of CHOU (1994), even though soon after, KOIWAYA (1995) questioned the current status of *A. morishitai* due to no obvious genital differences and pointed out the necessity of comparing it with the Vietnamese population of *A. amythaon* (WU 2017).

In addition to the taxonomic status of *A. morishitai* that can be called into question, the female of this species is quite mysterious and poorly documented. Although some females were recently recorded by WANG et al. (2020) and ZHOU et al. (2022), the source of images in both works was sometimes questionable. For example, *Faunis*



aerope (Leech, 1890) and *Stibochiona nicea* (Gray, 1846) in those two books were photographed from Guangdong and Jiangxi, respectively, rather than from Hainan (GU et al. 2018, LI & LIU 2022). Therefore, there is no female of *A. morishitai* with collection data guaranteed thus far.

Due to the field investigations by the second author of the present study, authorized by the Wu Zhishan Division of Hainan Tropical Rainforest National Park Bureau, a series of valuable *A. morishitai* specimens is available, including females, making further studies on this rare species possible. Thus, the present paper is devoted to reviewing the taxonomic status of *A. morishitai* and describing the female, including genital structure and DNA analysis results.

Material and methods

Material examined. The following subspecies of *A. amythaon* from the mainland are also examined for comparison with *COI* genes sequenced or obtained from NCBI and BOLD GenBank:

Amathuxidia amythaon annamensis Talbot, 1932 (TL: Annam, Vietnam): **VIETNAM:** Binh Thuận, Đông Tiến, vi.2022, 1 ♂ (Collection of Zhe Liu, Hainan, China, ZLHC; VNM-01; OQ324884); ditto, vi.2022, 1 ♀ (ZLHC; VNF-01; OQ324885). **CHINA: YUNNAN:** Xishuangbanna, 1 ♀ (Collection of Fei Lu, Sichuan, China; YNF-01). *Amathuxidia amythaon dilucida* (Honrath, 1884) (TL: Perak, Malacca): **MALAYSIA:** no locality, 1 ♂ (NCBI, EU528312); **SELANGOR:** Batu, 1 ♀ (NCBI, KF226270). **THAILAND:** Khao Chong, ♂ (BOLD, KHCBT1205-16).



Fig. 1. Habitus of *Amathuxidia amythaon* (Doubleday, 1847) subspecies. TLM-01 and TLM-02 – individuals from contact zones with intermediate phenotypes.

Amathuxidia amythaon amythaon (TL: Silhet): **THAILAND:** Kanchanaburi, Ampuh Sri Sawat, 1 ♂ (NCBI, ON436668).

Individuals with intermediate phenotypes: **THAILAND:** Phetchabun, 26.iv.2018, 1 ♂, Y. Inayoshi leg. (Collection of Yutaka Inayoshi, Chiang Mai, Thailand, YICT; TLM-01); Chaiyaphum, 24.iv.2018, 1 ♂, Y. Inayoshi leg. (YICT; TLM-02).

Terminology for genitalia follows KLOTS (1970) and PENZ (2021).

Molecular analyses. The *COI* gene is chosen for genetic distances and phylogenetic analyses. DNA extractions were conducted by Beijing Tsingke Biotech Co., Ltd (Beijing, China). The PCR reaction was applied in a 30 µL system by using 15 µL of Mix (I-5TM 2×High Fidelity Master Mix, Beijing Tsingke Biotech Co., Ltd.), 1 µL of gDNA, 12 µL of dH₂O, and 1 µL of each of forward and reverse primers (the general primers LCO1490 and HCO2198 utilized; FOLMER et al. 1994). The thermal profile of PCR consisted of a pre-denaturation at 98°C for 3 min, 37 cycles of denaturation at 98°C for 10 s, annealing at 55°C for 15 s, and elongation at 72°C for 15 s, then a final elongation at 72°C for 5 min.

Sequence matrices were aligned by Cluster W and edited manually using MEGA 11 (TAMURA et al. 2021). Genetic distances were also calculated in MEGA 11 by Kimura-2-parameter models (K2P) (KIMURA 1980), where 1000 replications for Bootstrap and gaps or missing data pairwise deletion were selected. Construction of the phylogenetic tree was performed using Maximum Likelihood (ML) analysis using IQ-TREE as implemented in the web online server (TRIFINOPOULOS et al. 2016), with branch support values evaluated based on 1000 replicates for SH-aLRT and ultrafast bootstrap. In addition, some satyr butterflies are selected for molecular comparison with their *COI* obtained from NCBI GenBank.

Results

The Hainan Island has been revealed to be once connected to N. Vietnam and S. China, approximately to the location of the Beibu Gulf, supported by biogeographical, palaeobotanical, palaeomagnetic, and volcanic evidence (ZHU 2016). Consequently, from a zoogeographical perspective, *A. morishitai* is undoubtedly more related to congeneric members from the mainland than to those limited to the islands of S.E. Asia. Thus, the subsequent taxonomic comparisons only involve the Hainan population and three continental subspecies of *A. amythaon*, i.e., *A. a. amythaon* from N.E. India to W. Thailand, *A. a. annamensis* from E. Thailand to Vietnam, and *A. a. dilucida* from S. Thailand to W. Malaysia, with other taxa excluded.

Considering distributional pattern and external characters, *A. morishitai* is not merely distributed close to the range of *A. amythaon annamensis* but also holds similar appearance, e.g., male hair tufts on the hindwing upperside are black and inconspicuous, and female yellow areas on the forewing upperside are developed (Fig. 1 and MONASTYRSKII 2011). Moreover, the molecular investigation also reveals the similarity of the two taxa with their mean K2P distance of only 0.8% in *COI* (Fig. 6). Hence, although *A. morishitai* is isolated geographically, both morphology and mtDNA

clarify that the divergence of this insular population is not very prominent from its Vietnamese lineage, confirming the conspecificity of *A. morishitai* and *A. amythaon annamensis*. For convenience, we designate these two eastern taxa as *annamensis*-group. Similarly, for the name-bearing subspecies *A. amythaon amythaon*, its topology is tangled with the peninsular representative *A. amythaon dilucida* and their *COI* differences vary from 0 to 0.2%, indicating they are also one species, a view supported by morphology as well because the latter is only distinguished from the nominotypical one by the blue band slightly broader (D'ABRERA 1985) (Fig. 6). Therefore, we included these two western taxa in another group, termed *amythaon*-group. Surprisingly, barcodes of these two groups differ by a moderate genetic distance, av. 2.8% (Fig. 6). Presently, the key to handling the taxonomic status of *A. morishitai* is whether the two groups are the same species. The distributional map depicted by INAYOSHI (2023) shows that *amythaon* and *annamensis* are quasi-allopatric with W. to C. Thailand as their contact zone (Fig. 5). Based on the sympatric record in W. Thailand (OKAMOTO et al. 2013), KIMURA et al. (2016) proposed that these two groups could be different species. However, in central parts of Thailand, individuals with phenotypes intermediate between *annamensis* and *amythaon* have been captured by Inayoshi and illustrated on his web (INAYOSHI 2023) (Fig. 1). These transitional forms imply that reproductive isolation between *amythaon* and *annamensis* has not been fully established; probably their genital similarity, especially in males, makes their natural interbreeding possible (AOKI et al. 1982, PENZ 2021, INAYOSHI 2023) (Fig. 4).

To sum up, according to the intermediate individuals from contact zones and the species delimitation criteria by LUKHTANOV et al. (2016), even if the *annamensis*-group shows a deeper divergence than normal on a subspecific level genetically, we hereby conservatively treat the two groups conspecific as traditionally arranged. Correspondingly, on the basis of morphological and molecular evidence, placing *morishitai* as a subspecies is preferable to a distinct species. Therefore, we formally downgrade *A. morishitai* to an insular subspecies of *A. amythaon* and redescribe it due to the poor and misleading original description.

Amathuxidia amythaon morishitai Chou & Gu, 1994, stat. nov.

(Chinese name: 交脉环蝶海南亚种)
(Figs 1–6)

Amathuxidia morishitai Chou & Gu, 1994 in CHOU (1994: 299, fig. for ♂ HT + 755, fig. 15 for ♂ genitalia). Type locality: Hainan.

Amathuxidia morishitai: CHOU (1998: 56, figs 5–8) (inaccurate wing venation, see in remarks); LANG (2012): 65 (notes); WU (2017): 696, fig. 01 (♂ with notes); WANG et al. (2020): 89 (♀); ZHOU et al. (2022): 37 (♀).

Amathuxidia amythaon spp.: KOIWAYA (1995): 12 (status discussion).

Material examined. *Amathuxidia morishitai* Chou & Gu, 1994. 4 ♂♂ 2 ♀♀, **CHINA: HAINAN:** Mt. Wuzhi, Wuzhishan, 31.iii.2020, 1 ♂, Z. Liu leg. (Collection of Wu Zhishan Division of Hainan Tropical Rainforest National Park Bureau, CWZS); ditto, 6.x.2019, 1 ♂, Z. Liu leg. (CWZS); ditto, 18.xi.2019, 1 ♂, Z. Liu leg. (CWZS); ditto, 22.vi.2022, 1 ♂, Z. Liu leg. (CWZS; voucher HNM-01; access number OQ324882); Jianfengling, 20.vi.2022, 1 ♀, Z. Liu leg. (CWZS; HNF-01; OQ324883); Mt. Wuzhi, 18.vii.2023, 1 ♀, Z. Liu leg. (CWZS; HNF-02).

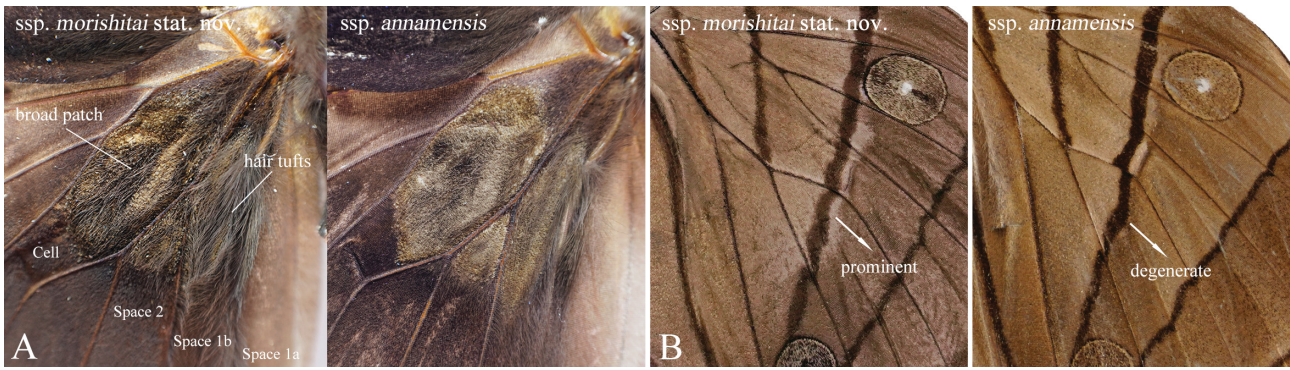


Fig. 2. Hindwing of *Amathuxidia amythaon* (Doubleday, 1847) subspecies. A – the sex brands. B – the white band along the outer edge of the postdiscal line.



Fig. 3. Photos of *Amathuxidia amythaon morishitai* Chou & Gu, 1994, stat. nov., in nature.

Description of female. External characters. Sexual dimorphism: Larger than male. Rows of spines on tibia in foreleg absent. Wing upperside ground color brown and duller. Forewing upperside with oblique yellow band from centre of costa to tornus and small ochre patch close to inner edge of yellow band in space 2. Hindwing upperside with marginal yellow patch reducing from apex to vein 2. Patterns of wing underside similar to those of males but tinged with deep brown (Fig. 1). **Genitalia.** Anterior edge of sterigma irregular with antrum sclerotized. Sterigma elongated posteriorly forming bifurcate projection. Projection excavated but less than half length of projection. Corpus bursa elliptical with two slender signa (Fig. 4).

Diagnosis. This insular subspecies can be separated from *A. a. annamensis* by the combination of the following characteristics (Figs 1–4):

- i) Oblique band on the forewing upperside is more tapering in males and narrower in females.
- ii) Apical yellow patch on the hindwing upperside is slightly more developed in females.
- iii) White band along the outer edge of the postdiscal line on the hindwing underside is often more prominent.
- iv) Excavation on the projection of sterigma is less deep.
- v) Absence of perfumed scent from the sex brands.

Stigma. Sex brands on the hindwing upperside are recognized as two kinds of specialized scales. One is a broad velvety patch covering the cell, base of spaces 1b and 2. As FRUHSTORFER (1911) noted, a pleasant scent emanates

from this patch leaving *A. amythaon* among the most perfumed butterflies. Such fragrance can also be detected in *A. a. annamensis*, but this synapomorphy is absent in *A. a. morishitai* stat. nov., a particular alteration in odor characteristics that has never been reported (Fig. 2). The second type of scales are hair tufts laying along vein 1b, which is black and inconspicuous in the *annamensis*-group, whilst brown and notable in the *amythaon*-group (D'ABRERA 1985, VAN DER POORTEN & VAN DER POORTEN 2020) (Fig. 2).

Biology. This insular subspecies can be encountered in dense forests mixed with bamboo at low to moderate elevations (alt. 200–700 m). Its time of activity is approximately from 9:00 a.m. to 14:00 p.m. and it likes to rest on foliage or trunks (Fig. 3).

Phenology. Multivoltine. Unexpectedly, this scarce subspecies has a wide flight period and can be found all year round (WU 2017; J. S. Lu & J. H. Lu, pers. comm. 2022; Lo, pers. comm. 2023).

Variations. The dorsum of the forewing in males is occasionally not protruded.

Larva and host. Both immature stages and host plants of the genus *Amathuxidia* are currently unknown, probably *Palmae* species serve as foodplants (CANTLIE 1952, IGARASHI & FUKUDA 1997).

Distribution. Endemic to Hainan Is. (China).

Remarks. The characters originally given and the illustration of wing venation provided by CHOU (1998) showed

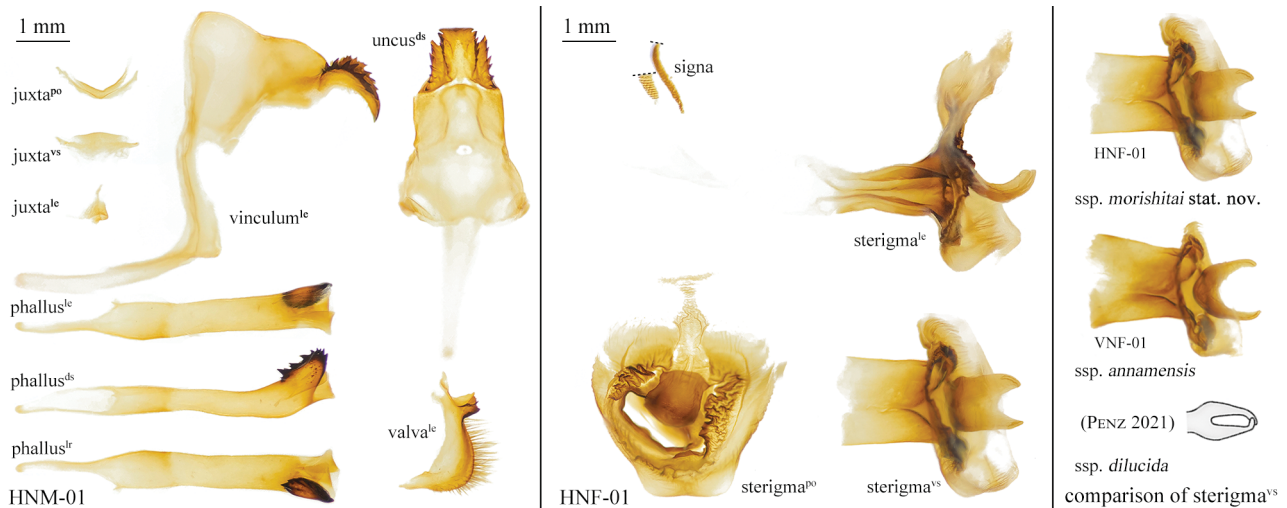


Fig. 4. Genitalia of *Amathuxidia amythaon morishitai* Chou & Gu, 1994, stat. nov. Abbreviations: ds – dorsal view, le – lateral left view, lr – lateral right view, po – posterior view, vs – ventral view.



Fig. 5. Distribution map of *Amathuxidia amythaon* (Doubleday, 1847) subspecies. Type localities are represented by the letter T (type locality of *A. a. annamensis* Talbot, 1932 was not given specifically). The localities of the specimens sequenced are marked on the map. Source from DOUBLEDAY (1847), HONRATH (1884), FRUHSTORFER (1911), EVANS (1932), TALBOT (1932), INAYOSHI (2023) and KUNTE et al. (2023).

that hindwing tornus in *A. a. morishitai* stat. nov. is not extended, which is regarded by Chou & Gu (CHOU 1994) as a major feature. However, examined materials from Hainan and other previous literature all pointed out that this insular population bears a tail on each hindwing that is not different from other sister taxa. Consequently, the holotype of *A. a. morishitai* stat. nov. is deemed to be

a worn individual whose tornus is lost, which probably misled Chou and Gu's judgment.

In addition to the Hainan subspecies, two other subspecies of *A. amythaon* can also be occasionally found in the frontiers of China: the nominotypical subspecies in S. Shannan, Xizang, photographed in KUNTE et al. (2023), and the Vietnamese subspecies offered for sale by some local

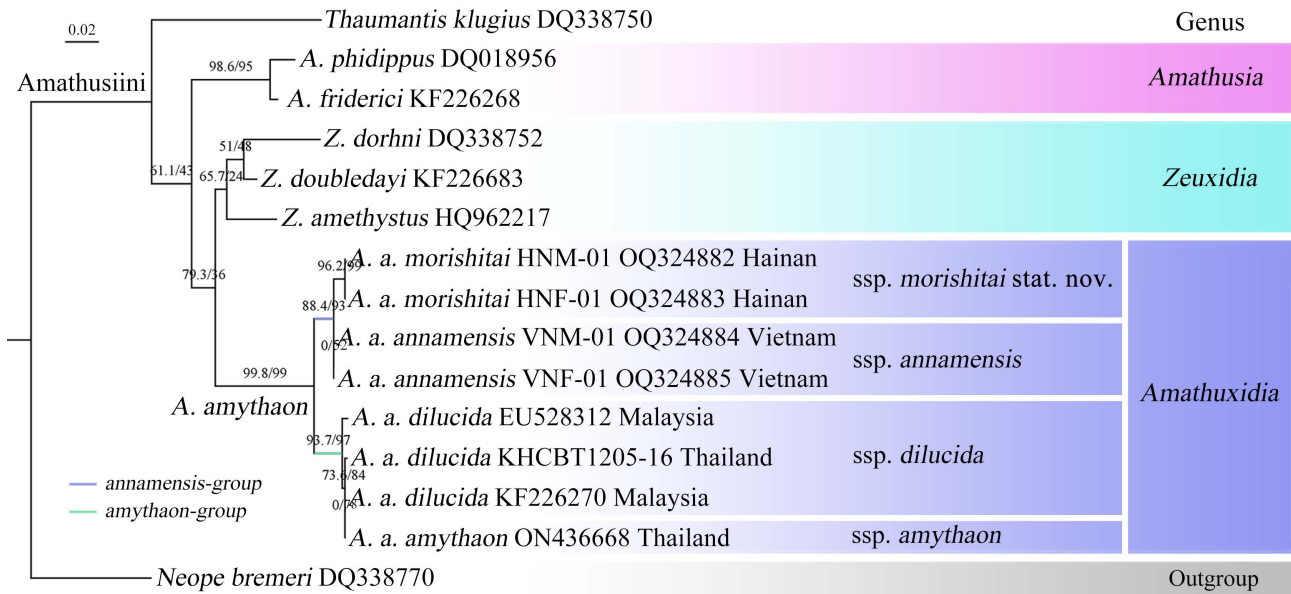


Fig. 6. Phylogenetic tree of the tribe Amathusiini inferred from ML analysis of *COI* with bootstrap support values (SH-aLRT /ultrafast bootstrap).

dealers who claim that it was collected from Xishuangbanna, S. Yunnan (Figs 1, 5). However, records of the two subspecies have not been formally documented, and further investigations in these areas are needed to enhance our understanding of Chinese biodiversity.

Discussion

With the development of technology, more approaches are embraced and integrated into taxonomy. Among them, molecular sequencing has brought a great convenience by breaking through the limitations of traditional morphology (DINCĂ et al. 2011). In the molecular results presented in this article, the genetic divergence in *COI* is moderate (2.8%), which is greater than the 2% specific discrimination threshold but below that of 3%. However, relying on a so-called threshold for species identification is arbitrary and sometimes even subjective as there is no absolute value that would allow distinguishing between species (HEBERT et al. 2003, LUKHTANOV et al. 2016, AHRENS et al. 2021). Therefore, it is ambiguous to determine whether the *annamensis*-group is worthy of a species status solely due to genetic distinctions. Given the homology in male genitalia, the intermediate individuals from transitional zone, quasi-allopatric distribution, and also considering the nomenclature stability advocated by ICZN, we continue to treat the *annamensis*-group and *amythaon*-group as a whole entity, pending a future evaluation using more rigorous and objective species delimitation criteria.

In the present study, the relationships of four subspecies of *A. amythaon* inhabiting areas of China and Indochina are discussed based on the molecular and morphological information. However, the overall analysis of this species is still incomplete, taking into account that considerable populations from islands of S.E. Asia were described and listed as members of other subspecies of *A. amythaon* (AOKI

et al. 1982, 2002). Some of these insular subspecies have particular morphological characters, e.g., *A. a. negrosensis* Schröder & Treadaway, 1980 that bears splendid marginal blue or *A. a. perinthis* Fruhstorfer, 1911, whose genitalia are quite different (AOKI et al. 1982). These subspecies may represent real separate species and a splitting attitude may be relevant. Anyway, this study is the first attempt to understand *A. amythaon* and also a starting point for any future research on this subject.

Acknowledgments

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