



On the taxonomic status of the endangered Benguet Swallowtail *Papilio benguetana* Joicey & Talbot, 1923 (Lepidoptera: Papilionidae)

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Abstract

A review of available evidence and new molecular data supports recognition of the endangered Benguet swallowtail butterfly *Papilio benguetana* Joicey & Talbot, 1923, endemic to the Island of Luzon in the northern Philippines, as a distinct species of *Papilio* and not a subspecies of the widespread *P. xuthus* Linnaeus, 1767 as previously suggested.

Key words: The Philippines, Cordillera, Luzon, Benguet, Swallowtail butterflies, Oriental region, Species delimitation

Introduction

Papilio benguetana was described in 1923 as a species in good standing by English entomologists James John Joicey and George Talbot based on a single male specimen collected by Percy Ireland Lathy on Santo Tomas Peak, Benguet district in North Luzon, the Philippines (Joicey & Talbot 1923). They described the new species as most closely related to, and with an appearance of, a “considerably modified derivative of *Papilio xuthus*” (Fig. 1). The type specimen is now at the Natural History Museum, London. Earlier specimens (five males) collected in 1912 by A. E. Wileman in Pauai, North Luzon, were later discovered at the Natural History Museum at Tring, erroneously reported as *P. xuthus* (Wileman 1914; Iwase 1966). In the following decades, attempts to acquire additional specimens of this rare and enigmatic butterfly yielded only more males, and the female remained elusive until 1965 when it was first collected by the Japanese researcher Motohiro Harada (Igarashi 1973). The butterfly flies in open areas on the high mountains from 1600 up to 2500 meters above sea level from March to June (Page and Treadaway 2003, 2004). Both sexes exhibit hill-topping behaviour, with the males flying more vigorously in patrolling territories.

Soon after its description in 1923, Baron Kurt von Rosen (in Seitz, 1929) referred to *benguetana* as “an interesting montane form” of *Papilio xuthus*: “... und wurde kürzlich in einer interessante Bergform auch auf Nord-Luzon (= *benguetana* Joic. & Talb.)”. This was perhaps interpreted by Tadao Kano (1933) as a subspecific designation for this taxon, as he used the combination *Papilio xuthus* subsp. *benguetana* in his works (Kano 1933, 1936). Some subsequent authors adopted this classification as well, and it further made its way to popular books and field guides (e.g. Jumalon 1968, 1969; Igarashi 1979; Fujioka *et al.* 1997; Page & Treadaway 2003, 2004; D’Abrera 2006). Nevertheless, the general consensus for the most part remained that *P. benguetana* was a good species, distinct from *P. xuthus* (e.g. Iwase & Kurosawa 1963; Iwase 1965, 1966; Harada 1966; Murayama & Okamura 1973; Morishita 1974; Ae 1978, 1988; Tsukada & Nishiyama 1980; D’Abrera 1982; Hancock 1983; Bridges 1988; Saitoh 1988; Racheli & Biondi 1989; Treadaway 1995, Yagi & Fujioka 2005, Hardy & Lawrence, 2017; Nakae 2021; Taga 2024). Throughout their landmark hybridization studies, Kodo Maeki and Shigeru A. Ae (1977–1979) also treated *benguetana* as a good species.

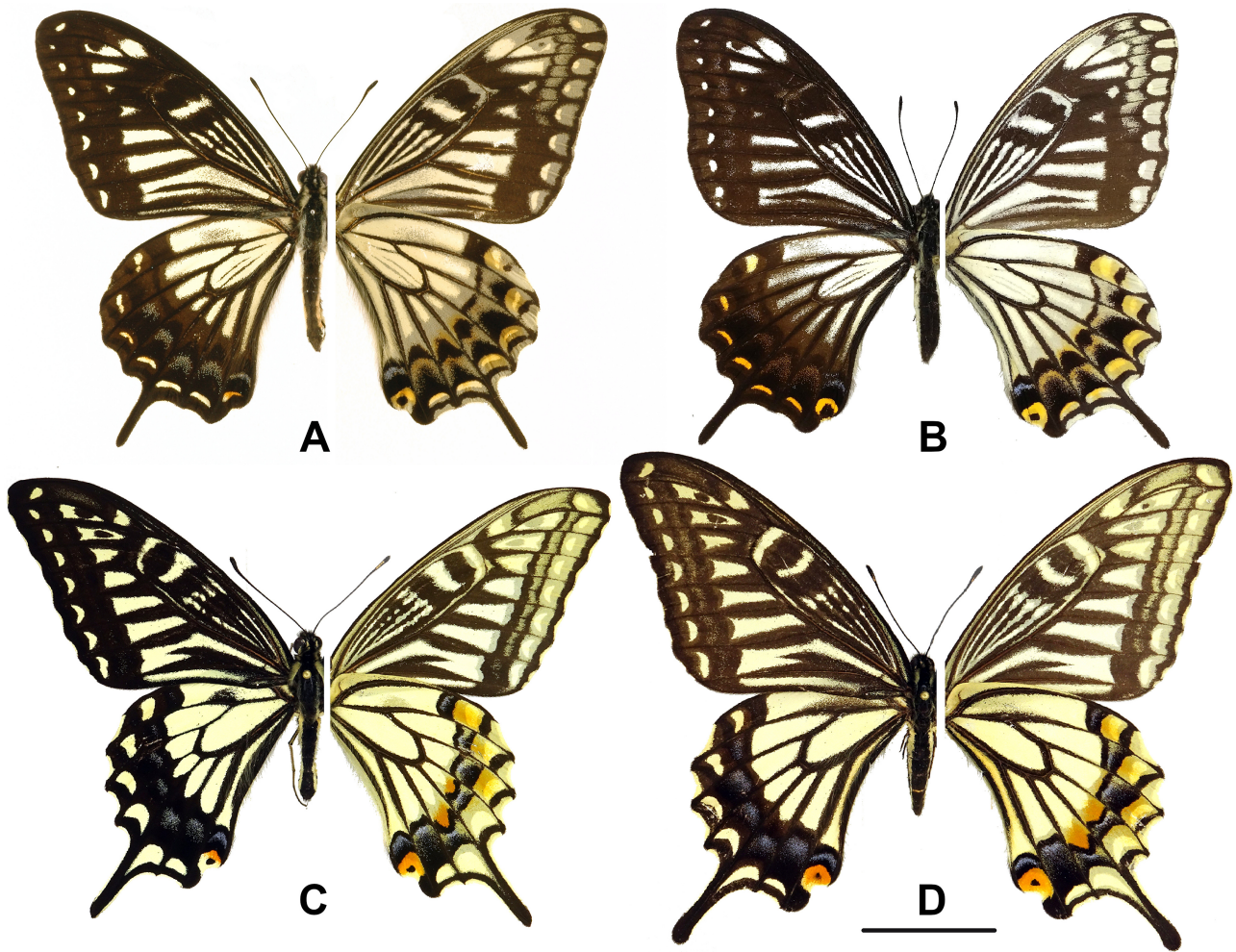


FIGURE 1. Adults of *P. benguetana* (A, B) and *P. xuthus* (C, D). Males (right) and females (left); upperside of the wings are shown on the right and underside of the wings on the left side. A) *P. benguetana* ♂, Philippines: Luzon. B) *P. benguetana* ♀, Philippines: Luzon. C) *P. xuthus* ♂, CDB-119, China, Yunnan. D) *P. xuthus* ♀, China: Sichuan. Scale bar is 2 centimeters.

The life history of *Papilio benguetana* is poorly known, and its larval host plant has remained undocumented. In 1979 Suguru Igarashi illustrated a first-instar larva of '*Papilio xuthus benguetana*', possibly from an unsuccessful rearing experiment, which appeared to be slightly different compared to the first-instar larva of *P. xuthus* (Igarashi 1979) (Fig. 2). However, in 1988 Ae reported a lack of differentiation in larval characteristics between *benguetana* and *xuthus* "... based on the observation of the 5th-instar larvae that I have been able to raise and the puparia in the Osaka Museum of Natural History ..." (Ae 1988).

In the same paper, Ae also cited his hybridization experiments in 1979 where he listed a crossing between *P. xuthus* and *P. benguetana* that resulted in 26 eggs and 5 males with an F_1 fertility of 50 (Ae 1979). A fertility value of 50 for the hybrids meant that one sex had good (perfect or almost perfect) fertility and the other sex was sterile. This suggested that the two species were not fully compatible, since for truly conspecific taxa (both sexes with perfect or almost perfect fertility), Ae's assigned value was 100.

Soon after, Tsukada & Nishiyama (1980¹) also listed '*Papilio benguetanus*' as a good species "... on the grounds that its markings differ greatly from those of *xuthus* in both sexes". They noted the successful hybridization with *P. xuthus* in which F_1 and F_2 were obtained, and similarities in genitalia between the two taxa, as the reasons why some past authors considered *benguetana* as a subspecies of *P. xuthus* (Tsukada & Nishiyama 1980) (Fig. 3). However, in 2004, referring to the work of Tsukada & Nishiyama, Page and Treadaway (2004) arrived at the opposite conclusion that *benguetana* should be treated as a subspecies of *P. xuthus*, "... in view of the lack of morphological differences in the genitalia of both sexes ... and the apparent close genetic relationship".

¹ The Japanese and English editions of the book by Tsukada & Nishiyama were published in 1980 and 1982, respectively.



FIGURE 2. First-instar larvae of *P. benguetana* (A) and *P. xuthus* (B), from Igarashi (1979).

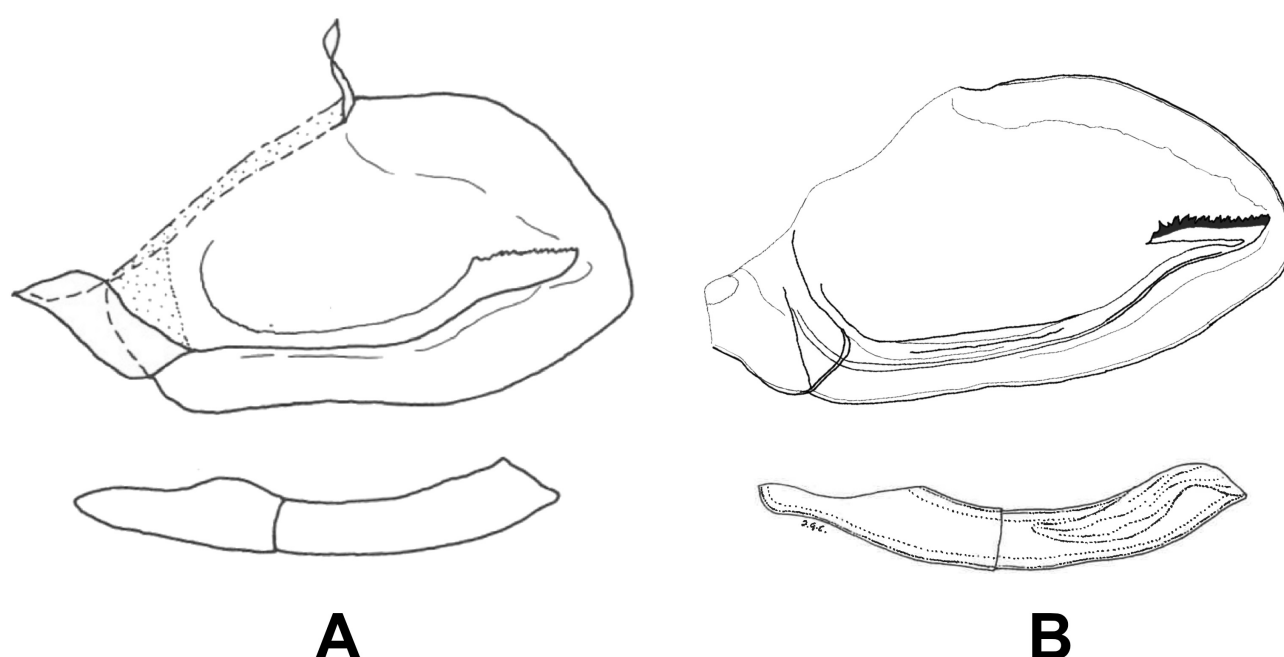


FIGURE 3. Comparison of male genitalia (left valve and phallus). A) *P. benguetana*, from Tsukada & Nishiyama (1980); drawing by H. Chiba. B) *P. xuthus*, South Korea, from Nazari *et al.* (2023).

Recent molecular studies have provided further evidence affirming the status of *benguetana* as an independent species (e.g. Miyakawa *et al.* 2017, 2018; Allio *et al.* 2021, Condamine *et al.* 2023). Nevertheless, the confusion continues to this day. In 2006, the government of the Philippines issued postal stamps with the subspecific combination ‘*P. xuthus benguetanus*’ (Nazari 2021). Some modern butterfly guidebooks still use the subspecies designation, or even both combinations (e.g. Sturm 2017). Popular online resources such as Lepiforum and Funet also continue to use the subspecies combination.

The hostplant utilized by *P. benguetana* under natural conditions remains unknown. Ae (1978) suggested *Euodia meliifolia* (Hance ex Walp.) Benth. (Rutaceae) as a potential candidate. Tsukada & Nishiyama (1980) stated that females of *P. benguetana* refused to oviposit on *Zanthoxylum* or *Citrus*, hostplants commonly used by *P. xuthus* in captivity (Shirôzu & Hara 1976; Fujioka *et al.* 1997; Hsu 2002; Suda *et al.* 2019). This observation suggests host usage has differentiated between *P. benguetana* and *P. xuthus*. Tsukada & Nishiyama (1980) stated that larvae hatched from eggs produced by an artificially manipulated female accepted *Phellodendron amurense* Rupr. (Rutaceae), a plant growing in temperate habitats in East Asia, not found in the Philippines (Zhang 2025).

Papilio benguetana has been listed as “Vulnerable” by Collins and Morris (1985) and “Near Threatened” by

the World Conservation Union (Gimenez Dixon 1996), and it is indexed in the Annex B of the EU-Regulation No. 2023/966 on the International Trade in Endangered Species of Wild Fauna and Flora (The European Commission 2023). However, it does not appear in any of the regional or national Red Lists in the Philippines (e.g. Gonzalez *et al.* 2018, RPDENR 2019). Like most Philippine endemics, the species is under intense pressures due to environmental degradation and human population growth, and it may be headed for extinction within the next several years along with the other Luzon endemic swallowtail, *Papilio chikae* Igarashi, 1965.

In this study, we re-examined available morphological evidence and used new molecular data from COI barcodes to verify the taxonomic status of *benguetana* by comparing its genetic distance from *P. xuthus* and other sister-species in the larger context of the tribe Papilionini.

Materials and Methods

Available data on *P. benguetana* from past literature, including illustrations of larvae by Igarashi (1979) and male genitalia by Tsukada & Nishiyama (1980), were re-examined. Legs were detached from three specimens of *P. benguetana* stored at The University Museum, The University of Tokyo (UMUT), collected on 15th October 2016 in the Philippines: Cordillera Administrative Region, Ifugao Province, North Luzon Island, Mayoyao (16.8721839, 121.2536492). Two of these samples were barcoded at the Yago lab in UMUT, and the third was submitted to the Center for Biodiversity Genomics in Guelph, ON, Canada, where it was barcoded using mini-primers (LepF/mLepR and mLepF/LepR) (Hajibabaei *et al.* 2006). Thirty-eight additional samples of *Papilio xuthus* from Japan, Korea, China, Taiwan and Vietnam, previously sequenced at UMUT or through this study, were also included in our analyses (Supplementary Information S1). All new sequences were submitted to GenBank (Accession PX064465–PX064527, PZ055775–PZ055777) (Supplementary Information S2) and are publicly available through the BOLD dataset “DS-BENGUET” (dx.doi.org/10.5883/DS-BENGUET). We created two datasets: First, for a haplotype network we supplemented our *P. benguetana* and *P. xuthus* sequences with 104 additional publicly available barcode sequences of *P. xuthus* on GenBank and BOLD. We conducted a Median-Joining Network in PopART (Bandelt *et al.* 1999) (Fig. 4) and calculated the uncorrected *p*-distances in MEGA 11.0.8 (Tamura *et al.* 2021). We also carried out an Assemble Species by Automatic Partitioning (ASAP) analysis on this dataset using the ASAP web application (<https://bioinfo.mnhn.fr/abi/public/asap/asapold.html>) under JC69, K80, and *p*-distance models (Puillandre *et al.* 2021) (Supplementary Information S3).

For our phylogenetic analysis, we created a second dataset selecting nineteen species of *Papilio* representing all subgenera within this genus with a focus on the *machaon* group. In order to reinforce the backbone of the phylogeny, in addition to the COI-COII sequences, we mined available sequence data for 15 additional gene regions (ND5, ND1, 16S, large subunit ribosomal RNA, EF-1 α , wingless, GAPDH, MDH, IDH, RPS5, CAD, H3, Arginine-Kinase, and engrailed) made available through previous studies and genomic sequencing (Table 1). Alignment of sequences was done using MUSCLE modules implemented in AliView 1.28 (Larsson 2014) and double-checked visually. The final length of our dataset was 16,664 base pairs. Bayesian phylogenetic inference was conducted in BEAST 2.7.3 (Suchard *et al.* 2018) under GTR substitution model and an optimized relaxed clock, with a chain-length of 20 million generations. We constrained the phylogeny using secondary calibration points following Kawahara *et al.* (2023) and Condamine *et al.* (2023) by fixing the split of the most recent common ancestors (MRCA) of *P. polyxenes* and *P. zelicaon* at 1–3.5 MYA (offset:1), *P. clytia* and *P. glaucus* at 19–23 MYA (offset:0.5), and *P. thoas* from others at 27–30 MYA (offset:1). Convergence of the posterior distributions was then evaluated using TRACER v1.7.1 (Rambaut *et al.* 2018), convergent chains were combined using LogCombiner with a burn-in of 20% and the consensus tree was generated using TreeAnnotator v2.7.3 (Heled & Bouckaert 2013).

Results

Morphological results. The adults of *P. benguetana* are easily and unambiguously distinguishable from *P. xuthus* by their rounded wings and more extensive black markings on both wings (Fig. 1). A close re-examination of the detailed illustrations by Igarashi (1979) of the first-instar larvae of *P. benguetana* and *P. xuthus* showed minor differences not only in coloration, but also in the dimensions of the first two thoracic segments (Fig. 2).

TABLE 1. GenBank accessions for taxa and gene regions used for the phylogenetic analysis (Fig. 5). For data related to the Haplotype network (Fig. 4), see Supplementary Information S2.

Subgenus	selected species	COI-COII	ND5	NDI	16S	large subunit rRNA	EF-1a	wingless	GAPDH	MDH	IDH	RPSS	CAD	H3	Arg-Kin	engrailed	
<i>Achillides</i>	<i>Papilio paris</i>	AY457574	NC_053770	NC_053770	JQ982234	OQ927990	AY457605	AY569116	-	-	-	-	-	-	-	KJ458922	
<i>Alexanoria</i>	<i>Papilio alexanor</i>	AF044012	GQ268385	AJ224090	GQ268343	AJ224052	AF044821	GQ268407	DWLR-	DWLR-	DWLR-	DWLR-	DWLR-	DWLR-	DWLR-	SRR8954526	
<i>Araminta</i>	<i>Papilio demolion</i>	KX557503	-	-	KX557715	-	KX557944	KX558134	01031729	01016358	01000277	01078964	01002862	01003219	01010201	-	
<i>Chilasa</i>	<i>Papilio clytia</i>	AY457594	GQ268387	AJ224095	DQ673337	AJ224057	AY457606	GQ268408	-	-	-	-	-	-	-	-	
<i>Dnryia</i>	<i>Papilio dardanus</i>	AY457584	GQ268383	AJ224097	AF095451	AJ224059	AY457612	GQ268405	QDHC-	QDHC-	QDHC-	QDHC-	QDHC-	QDHC-	QDHC-	AS-	
<i>Eleppone</i>	<i>Papilio anactus</i>	AY457592	-	AJ224091	-	AJ224053	AY457608	AY569120	01004189	01007041	01003693	01001697	01000144	01004862	01002621	M1318645v1	
<i>Euchenor</i>	<i>Papilio euchenor</i>	KX557527	-	-	KX557741	-	KX557950	KX558160	-	-	-	-	-	-	-	-	
<i>Heraclides</i>	<i>Papilio thoas</i>	AY457601	DQ351049	NC_059755	DQ351089	DWLMW-01001473	AY457632	AY569126	DWLMW-01058571	01002307	01050290	01001809	01025167	01004505	01003642	SRR8954522	
<i>Menelaides</i>	<i>Papilio polytes</i>	AY457580	ABI00044	EU783952	DQ673341	NC_024742	NW_013525069	AY569119	NW_013526027	NW_013525270	NW_013527915	NW_013527359	NW_013527915	NW_013527137	AK402526	KJ458909	
<i>Nireopapilio</i>	<i>Papilio oribazus</i>	AY457591	-	-	-	-	AY457626	AY569119	-	-	-	-	-	-	-	-	KJ458871
<i>Papilio hospiton</i>	<i>Papilio hospiton</i>	AF044009	KJ936903	KT230686	-	AJ224108	AF044830	-	-	-	-	-	-	-	-	-	-
<i>Papilio indra</i>	<i>Papilio indra</i>	AF044011	LC274591	AJ224100	-	AJ224062	AF044824	-	-	-	-	-	-	-	-	-	-
<i>Papilio machaon</i>	<i>Papilio polyxenes</i>	AF044006	LS975121	AF229932	AF214632	AJ224107	AF044828	AY569124	NC_060000	NC_059992	NC_059989	NC_059988	NC_059989	NC_059995	NC_059987	iPapMach1	
<i>Papilio zelicaon</i>	<i>Papilio demolens</i>	AF044010	EF624026	JAOPJD-010008189	JN800551	ASM-2616782v1	AF044823	JAOPJD-01000001	JAOPJD-01000007	JAOPJD-01000030	JAOPJD-01000027	JAOPJD-01000023	JAOPJD-01000027	JAOPJD-01000002	JAOPJD-01000012	AS-M2616782v1	
<i>Priniceps</i>	<i>Papilio demolens</i>	AF044008	EF624025	AJ224106	-	DWLMW-01001327	AF044827	DWLMW-01000845	DWLMW-01007821	DWLMW-01019133	DWLMW-01014203	DWLMW-01026568	DWLMW-01008885	DWLMW-01020603	DWLMW-01013064	SRR8954529	
<i>Perourus</i>	<i>Papilio glaucus</i>	AY569092	AB013159	AJ224099	DQ351090	AJ224061	AY569104	AY569115	JAGSMY-01000001	JAGSMY-01000002	JAGSMY-01000016	JAGSMY-01000012	JAGSMY-01000016	JAGSMY-01000013	JAGSMY-01000017	kiz_Pde_v1	
<i>Sinopriniceps</i>	<i>Papilio benguetana</i>	AF044013	GQ268384	GQ268371	GQ268342	JWHW-01015497	AF044826	GQ268406	JWHW-01053466	JWHW-01038862	JWHW-01002376	JWHW-01048064	JWHW-01015791	JWHW-01015265	JWHW-01048385	pgl_assem-bly_v1	
<i>Sinopriniceps</i>	<i>Papilio xuthus</i>	PX064480	LC274592	-	-	-	-	-	-	-	-	-	-	-	-	-	
		AF043999	AB013149	AJ224105	LC801709	AJ224067	AF044838	AY569123	NW_013533657	NW_013529697	NW_013529869	NW_013530969	NW_013529869	NW_013531107	NW_013532703	KJ458908	

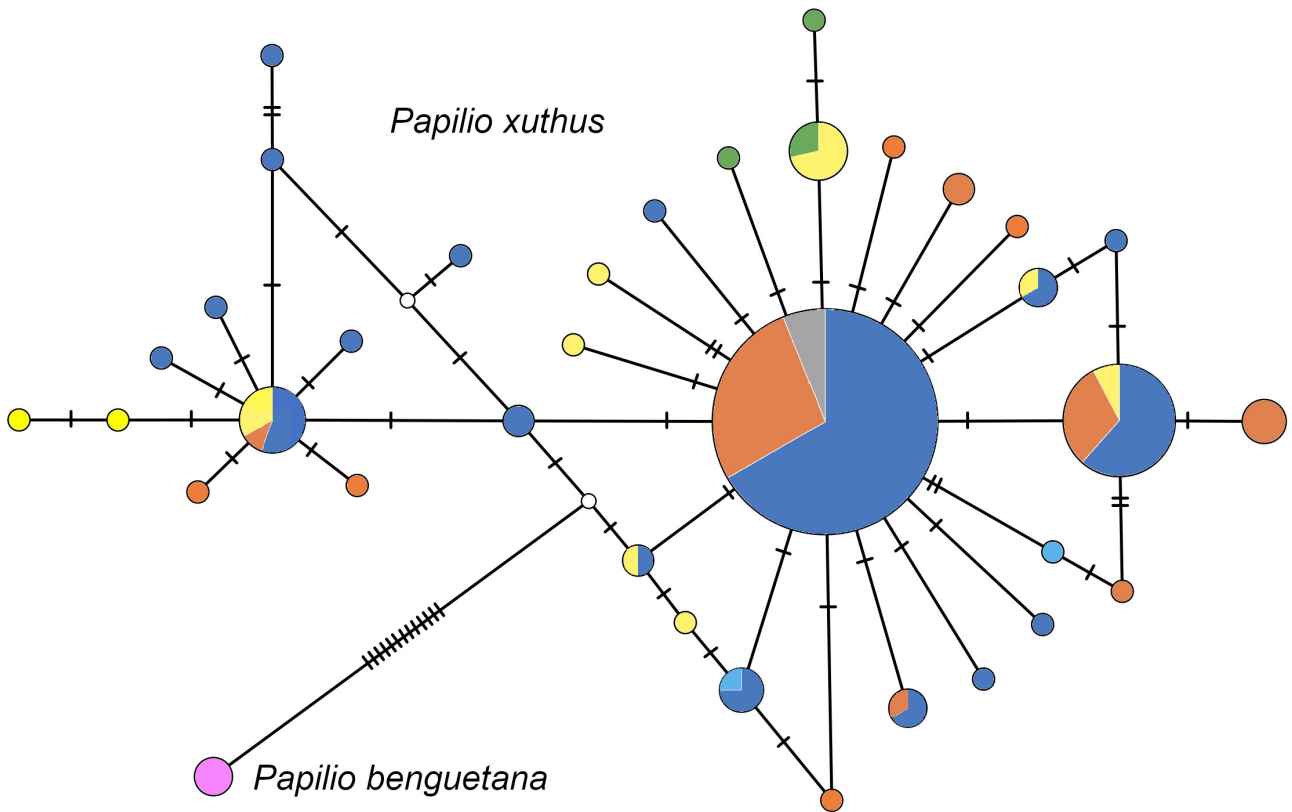


FIGURE 4. Median-Joining Network of COI barcodes for three *P. benguetana* (purple) and 195 samples of *P. xuthus*. Blue: South Korea (n=97), orange: China (n=67), yellow: Japan (n=15), azure: Vietnam (n=6), green: Taiwan (n=7), gray: unknown locality (n=3).

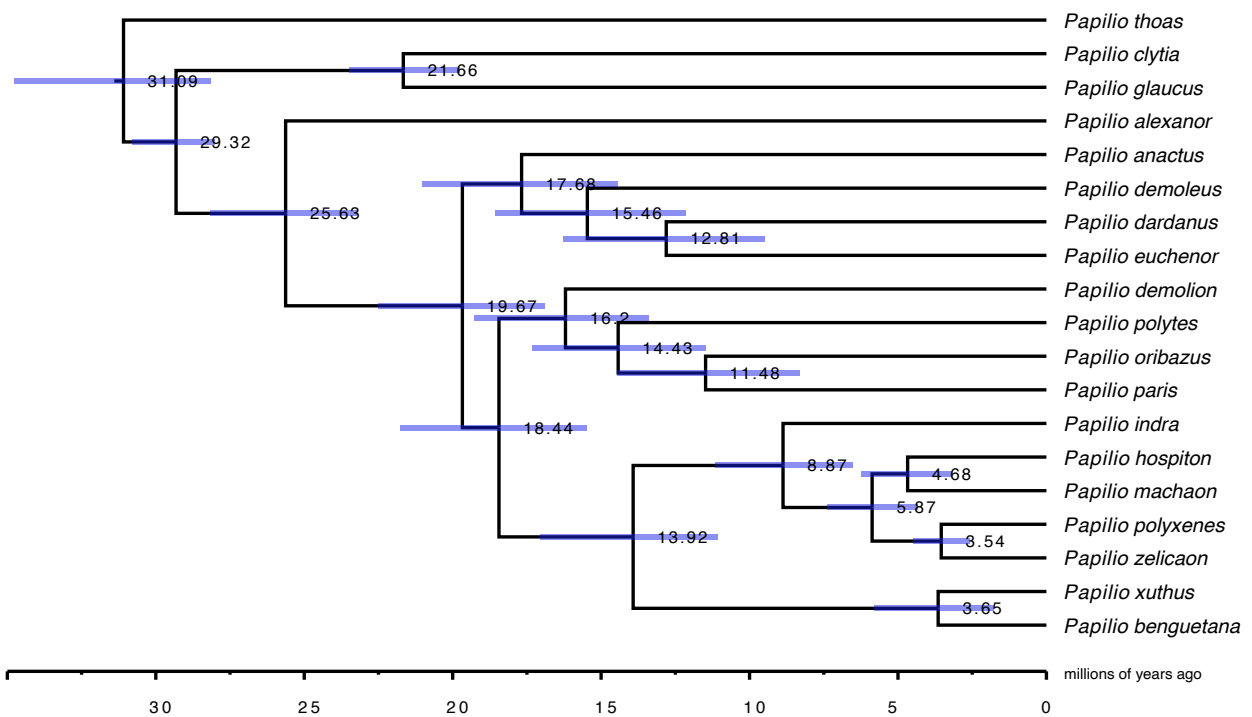


FIGURE 5. Multigene BEAST phylogeny of *Papilio*. Values represent mean node ages. For Bayesian posterior probabilities see Supplementary Information S4.

TABLE 2. Comparative average uncorrected COI *p*-distances between pairs of taxa in Papilionini included in Figure 5.

	<i>Papilio thoas</i>	<i>Papilio clytia</i>	<i>Papilio glaucus</i>	<i>Papilio alexanor</i>	<i>Papilio anactus</i>	<i>Papilio demoleus</i>	<i>Papilio dardanus</i>	<i>Papilio euchenor</i>	<i>Papilio demolion</i>	<i>Papilio polytes</i>	<i>Papilio oribazus</i>	<i>Papilio paris</i>	<i>Papilio indra</i>	<i>Papilio hospiton</i>	<i>Papilio machaon</i>	<i>Papilio polyxenes</i>	<i>Papilio zelicaon</i>	<i>Papilio xuthus</i>	<i>Papilio benguetana</i>
<i>Papilio thoas</i>																			
<i>Papilio clytia</i>	11.4%																		
<i>Papilio glaucus</i>	9.3%	7.6%																	
<i>Papilio alexanor</i>	10.3%	12.5%	10.5%																
<i>Papilio anactus</i>	10.2%	10.8%	10.0%	11.7%															
<i>Papilio demoleus</i>	10.5%	10.9%	9.1%	10.6%	7.4%														
<i>Papilio dardanus</i>	10.8%	12.2%	10.3%	10.9%	9.7%	7.9%													
<i>Papilio euchenor</i>	11.9%	11.2%	9.7%	12.8%	9.3%	8.7%	9.3%												
<i>Papilio demolion</i>	11.2%	11.2%	9.9%	13.2%	9.7%	9.6%	11.4%	9.7%											
<i>Papilio polytes</i>	11.9%	10.5%	10.0%	12.8%	10.2%	7.9%	9.7%	10.6%	9.3%										
<i>Papilio oribazus</i>	11.4%	12.6%	10.9%	13.8%	10.2%	9.1%	12.3%	11.4%	10.8%	10.6%									
<i>Papilio paris</i>	9.6%	9.9%	7.9%	11.7%	8.8%	6.2%	9.6%	8.8%	9.1%	7.8%	7.6%								
<i>Papilio indra</i>	10.0%	10.9%	8.8%	12.0%	7.8%	7.8%	8.8%	9.4%	9.4%	9.7%	9.3%	6.8%							
<i>Papilio hospiton</i>	8.7%	9.3%	7.9%	12.0%	6.7%	7.0%	8.4%	8.2%	9.0%	8.2%	7.9%	5.0%	4.7%						
<i>Papilio machaon</i>	8.8%	10.3%	8.4%	11.2%	7.3%	7.8%	9.3%	9.3%	9.3%	8.8%	9.6%	6.5%	5.3%	3.8%					
<i>Papilio polyxenes</i>	9.7%	9.6%	8.4%	11.9%	6.8%	7.8%	8.5%	8.8%	9.3%	9.1%	9.1%	7.0%	6.1%	4.0%	4.3%				
<i>Papilio zelicaon</i>	9.0%	10.8%	8.1%	11.6%	7.3%	7.4%	8.7%	9.4%	9.7%	9.3%	9.4%	6.7%	5.2%	3.5%	4.3%	3.2%			
<i>Papilio xuthus</i>	8.5%	10.2%	8.2%	12.3%	8.2%	7.6%	10.6%	9.6%	10.0%	10.0%	10.6%	7.9%	7.9%	7.1%	7.0%	7.4%	7.1%		
<i>Papilio benguetana</i>	9.0%	10.3%	8.4%	12.0%	8.5%	8.1%	10.8%	9.4%	10.6%	10.3%	11.6%	8.4%	8.5%	7.4%	7.8%	8.4%	8.2%	8.2%	2.6%

The male genitalia of *P. benguetana* and *P. xuthus* appear to be very similar (Fig. 3).

Molecular results. The uncorrected COI distance between *benguetana* and *xuthus* was found to be 1.98–3.78% (average: 2.6%), comparable to the distance between *P. zelicaon* and *P. polyxenes* (Table 2). Thirty-three haplotypes were observed within *P. xuthus*, with several haplotypes shared among China, South Korea, Japan, Taiwan, and Vietnam. The unique haplotype of *benguetana* showed thirteen mutations relative to *xuthus* on the Median-Joining Network (Fig. 4).

The best (lowest) ASAP scores were obtained for all three models when the subsets were $n=2$ species, separating the three *P. benguetana* samples from all *P. xuthus* (Supplementary Information S3). Our phylogenetic inference placed *P. benguetana* and *P. xuthus* as strongly supported sister-species, and our molecular clock analysis suggested that the MRCA of the two species split around 3.65 MYA (95% HPD height: 1.77–5.79 MYA) (Fig. 5; Supplementary Information S4). This date is somewhat older than that predicted by Condamine *et al.* (2023) (~1.5 MYA) and is comparable, for example, to the age of the split in the MRCA of *P. polyxenes* and *P. zelicaon* in our analysis (3.54 MYA) (Fig. 5).

Discussion

Differentiation at species level. Compared to other sibling species-pairs in the genus *Papilio*, the observable morphological differences between *P. benguetana* and *P. xuthus* are much more pronounced, supporting their distinct taxonomic status. The adults of these two species are readily distinguishable from one another using wing characteristics, while this is not nearly as easy in some other species-groups, e.g. among members of the Holarctic *P. machaon* group (Dupuis & Sperling 2020, Nazari *et al.* 2023), or in the Asian-Afrotropical *P. demoleus* group (Zakharov *et al.* 2004). Similar to *P. benguetana* - *P. xuthus*, members of these other sibling groups often show very little differentiation in their early life stages and/or genitalia. Poor differentiation of genitalia characteristics in butterflies of this group is well documented (Nazari *et al.* 2023, Todisco *et al.* 2025).

Genetically, a 2.6% distance in mtDNA sequences between *benguetana* and *xuthus*, which exceeds the average distance among conventionally recognized species in Papilionini, suggests that the two taxa represent independent evolutionary lineages at the species level. This is further supported by the results of an ASAP analysis (Supplementary Information S3).

Historical Biogeography. Our results suggest that the split in the ancestral stock of *P. benguetana* and *P. xuthus* occurred around 3.65 MYA, older than the date inferred by Condamine *et al.* (2023) (i.e. 1.5 MYA). Dates inferred by the latter authors for other nodes in their phylogeny for *Papilio* are also comparatively younger than those presented in our study, and their tree topology is also somewhat different. These discrepancies are probably due to the fact that we used a much smaller set of representative species for our phylogenetic analysis with a wider range of gene sequence data to strengthen the backbone of our phylogeny.

Papilio xuthus has a wide distribution across the eastern Palearctic, from the Far East of Russia to Central and Eastern China, Korea, Japan, northern Myanmar, Taiwan, and northern Vietnam. It has also been introduced to the Northern Mariana Islands and Hawaiian Islands (Nazari *et al.* 2023). Its range has been predicted to decline significantly in the future due to climate change, especially in China (Liu *et al.* 2025). The butterfly displays a range of seasonal and altitudinal variation, and despite some geographic differences noted in the female genitalia, currently it has no recognized subspecies. The range of nominotypical *P. xuthus* does not extend to the Philippines (Hardy & Lawrence 2022), and the closest populations occur in Taiwan.

A dispersal of the ancestral stock of *P. xuthus*-*P. benguetana* into Luzon from Taiwan would have been possible through the proposed arc-trench system known as the ‘Luzon Arc’ that formed during the early-middle Miocene, probably connecting Taiwan and Luzon from the late Miocene to the late Pliocene (ca. 10-2 Ma, Honza & Fujioka 2004) and facilitated the spread of different organisms (Nazari *et al.* 2024). Similar scenarios have been proposed, for example, for the dispersal of the ancestral stock of *Papilio dialis* and *P. hermeli* from Taiwan to the Philippines through the Luzon Arc followed by a vicariance event that separated the two lineages (Condamine *et al.* 2013), or the *Potanthus flavus* + *diffusus* + *niobe* group (Hesperiidae) (Hsu *et al.* 2005).

Since the early life stages of *P. benguetana* are not yet thoroughly documented, many lingering questions still remain unanswered. However, all available evidence strongly points to the presence of a distinct evolutionary lineage that has differentiated from *P. xuthus* at species level. More field and laboratory work are needed in order

to discover, rear and document its complete life cycle, and future genomic studies will undoubtedly shed additional light on the unique characteristics of this endangered swallowtail butterfly.

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Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper.

Supplementary Information S1. Distribution of samples used in the COI haplotype network analysis.

Supplementary Information S2. Specimen Data and GenBank Accessions.

Supplementary Information S3. ASAP results under JC69 (A), K80 (B) and *p*-distance C) models.

Supplementary Information S4. BEAST tree with node support values.