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● On the mysterious *Papilio prexaspes bowringi* Prout, 1919 from Hainan, China (Lepidoptera: Papilionidae)

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**Abstract:** The mysterious swallowtail *Papilio prexaspes bowringi* Prout, 1919 from Hainan Island, China was rediscovered since its last record at the end of the previous century. Its appearance and genitalia of both sexes, together with molecular data, are provided. The systematic position and taxonomic status of this little-known taxon were analyzed and clarified. The distributional map and molecular phylogeny of *P. prexaspes* C. Felder & R. Felder, [1865] are also illustrated with discussion.

**Keywords:** genitalia, Papilioninae, Papilionini, phylogeny

● 中国海南岛普瑞凤蝶海南亚种考证（鳞翅目：凤蝶科）

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**摘要:** 产于中国海南岛的神秘种群, 普瑞凤蝶海南亚种 (*Papilio prexaspes bowringi* Prout, 1919), 自上世纪末最后一次记录以来被重新发现。本文提供了该亚种两性成虫的外部形态特征、生殖器结构及分子数据, 并对这一鲜为人知类群的系统地位和分类学地位进行了分析与厘定。同时, 本文提供了普瑞凤蝶的分布图和分子系统发育树并进行了探讨。

**关键词:** 外生殖器, 凤蝶亚科, 凤蝶族, 系统发育

## ● Introduction

Based on a single male collected by Mr. C.T. Bowring, a little-known swallowtail from Hainan Island, China was described as a subspecies of *Papilio fuscus* Goeze, 1779, namely ssp. *bowringi* Prout, 1919. However, the external resemblance of *P. fuscus* with other similar congeners has confused past researchers, which resulted in the taxonomic status of some taxa, including *bowringi*, varying in different systematic arrangements (Jordan 1908–1909; Joicey & Talbot 1924). By examination of genital structures, Hancock (1983b, 1992) separated ‘*P. fuscus*’ from areas around Indochina to Indonesia as a distinct species with *prexaspes* C. Felder & R. Felder, [1865] as their senior name under subgenus *Menelaides* Hübner, [1819] of *Princeps* Hübner, [1807]. Based on molecular studies, modern revisional classifications supported the separation of *prexaspes* at specific level but suggested its genus-group name should be *Papilio* (*Menelaides*) rather than *Princeps* (*Menelaides*) (Joshi & Kunte 2022; Condamine *et al.* 2023). Thus, the Hainan representative was listed as a subspecies of *P. prexaspes* on zoogeographic grounds, viz., *P. prexaspes bowringi* (Hancock 1992; Zhu 2016).

Although this insular taxon was described over a century ago and many works on Chinese butterflies were compiled during these years, the little-known *P. p. bowringi* was only rediscovered in the book of Gu & Chen (1997) with illustrations. Hereafter, no further records were reported in subsequent works, such as Wu (2001) and Hu (2017), leaving *P. p. bowringi* as one of the most mysterious butterflies of the subfamily Papilioninae in China. Fortunately, it is certain that this species on Hainan has not become extinct since a few individuals have been captured and deposited in some private collections or even auctioned online (H Huang pers. comm.).

Recently, with the joint efforts of authors in this article, some individuals of *P. p. bowringi* became available from W. Hainan, including a previously unreported female. Therefore, the present study aims to supplement the knowledge of this insular taxon by posting its adults and genitalia, clarifying its taxonomic status, and discussing its relationship with other related taxa.

## ● Material and methods

Four ♂♂ and one ♀ of *Papilio prexaspes bowringi* from Hainan were examined and some of which were dissected and sequenced (Collection of Z. Liu, CZL hereafter; vouchers PB1–PB5; accession numbers PQ213159–PQ213161, PQ213861–PQ213863 for PB1–PB3). All subspecies of *P. prexaspes* were also analyzed by examining the illustrations given in previous works, including (i) ssp. *prexaspes* C. Felder & R. Felder, [1865] figured in the original description, Distant (1882–1886), D’Abrera (1982), Tsukada & Nishiyama (1980), van der Poorten & van der Poorten (2020), and Smetacek *et al.* (2024); (ii) ssp. *andamanicus* Rothschild, 1908 figured in Moore (1901–1903), Jordan (1908–1909), D’Abrera (1982), Tsukada & Nishiyama (1980), Nakae (2021), Inayoshi (2024), Kunte *et al.* (2024), and Smetacek *et al.* (2024); (iii) ssp. *dayacus* Rothschild, 1908 figured in Tsukada & Nishiyama (1980); (iv) ssp. *duboisii* Vitalis, 1914 figured in Hancock (1992), Monastyrskii (2007), Miyazaki *et al.* (2007), and Inayoshi (2024); (v) ssp. *pitmani* Elwes & Nicéville, [1887] figured in the original description, Moore (1901–1903), Smart (1975), D’Abrera (1982), Haugum & Collins (1987), Osada *et al.* (1999), Kimura *et al.* (2011), Sheela *et al.* (2019), and Inayoshi (2024); and (vi) ssp. *bowringi* figured in Gu & Chen (1997). Additionally, photos of type specimens of all the listed taxa except *duboisii* Vitalis, 1914, which is not extant, were examined, as well as specimens in the collection of the second author. All the above literature is also a source of distributional data, with some additional records from Gu (2002), Pang *et al.* (2016), and H Huang (pers. comm.).

Terminology for genitalia follows Klots (1970). The nomenclature of wing markings and venation refers to the work of Racheli & Bozano (2024). The name *pitmani* [originally *pitmanii*] was treated as a correct spelling in this study since its prevailing usage with attribution to the original publication (Cotton & Racheli 2006; Article 33.3.1 of the ICZN 1999). The publication dates of Hübner (1806–1819, 1816–1826), C. Felder & R. Felder (1865–1867), Elwes & Nicéville (1887), and Jordan (1908–1909) are based on ICZN (1987), Higgins (1963), The Natural History Secretary (1886–1887), and Griffin (1936) respectively.

Mitochondrial *COI* and nuclear *EF-1 $\alpha$*  were chosen for molecular analyses. DNA extractions were conducted by Beijing Tsingke Biotech Co., Ltd. (Beijing, China). The PCR reaction was applied in a 50  $\mu$ L system by using 25  $\mu$ L of Mix (2\**T8* High-Fidelity Master Mix, Beijing Tsingke Biotech Co., Ltd.), 5  $\mu$ L of gDNA, 16  $\mu$ L of ddH<sub>2</sub>O, and 2  $\mu$ L of each of forward and reverse primers. The thermal profile of PCR consisted of a pre-denaturation at 98°C for 3 min, 35 cycles of denaturation at 98°C for 10 s, annealing at 50–60°C (based on primers) for 10 s, and elongation at 72°C for 10 s, then a final elongation at 72°C for 5 min. The primers LepF1/LepR1 (Ta=55°C) and Jerry/Pat2 (Ta=50°C) were utilized for *COI* and EF135/EF684 (Ta=60°C) and EF51.9/EFrcM4 (Ta=55°C) for *EF-1 $\alpha$*  (Simon *et al.* 1994; Sperling *et al.* 1996; Hebert *et al.* 2004; Kandul *et al.* 2004; Braby *et al.* 2006).

Sequence matrices were aligned by Clustal W and manually edited using MEGA 11 (Tamura *et al.* 2021). The inter-fragment gaps within genes, caused by primer-induced discontinuities, were identified through congener alignment. Phylogenetic analyses were conducted using maximum likelihood (ML) and Bayesian inference (BI) approaches in PhyloSuite (Zhang *et al.* 2020; Xiang *et al.* 2023). Two molecular markers, *COI* and *EF-1 $\alpha$* , were analyzed as independent partitions with edge-unlinked models. The best-fit substitution models (TIM2+F+I for ML, GTR for BI) were selected using ModelFinder under the BIC criterion (Kalyaanamoorthy *et al.* 2017). Unrooted trees were initially constructed, then rooted using outgroups, with 1000 ultrafast bootstrap replicates for ML and 5 million generations for BI analyses. All other parameters retained their default configurations. The molecular analysis also included some related taxa with their genes mainly sequenced in Joshi & Kunte (2022) (Table 1).

## ● Results

The taxon *pitmani* was once considered an independent species due to its peculiar markings, particularly compared with its sibling *P. prexaspes* in adjacent regions but Hancock (1992) first included it as a subspecies of *P. prexaspes*. Recent molecular studies confirmed that it belongs to the species *P. prexaspes* as demonstrated by Joshi & Kunte (2022), a relationship somewhat parallel to that between *P. hipponous* C. Felder & R. Felder, 1862 and *P. fuscus* regarding genetic distances (Fig. 6). However, the latter two species not only originate from distinct zoogeographical regions but also are furnished with different genital structures, both of which strongly supports *P. hipponous* as a full species (Wallace 1876; Hancock 1992) (Fig. 6). Instead, the homology of male genitalia and the absence of certain molecular data, such as DNA sequences of *duboisii*, make it difficult to evaluate the taxonomic status of *pitmani* (Racheli & Haugum 1983; Hancock 1992; Monastyrskii 2007) (Fig. 6). Fortunately, additional evidence is an individual from the boundary between *pitmani* and *P. prexaspes* in S. Thailand, which exhibits an intermediate phenotype as noted by Inayoshi (2024), implying that the reproductive isolation has not been fully established (see a similar case in Li *et al.* 2024) (Fig. 5). Hence, given the allopatric distribution and transitional individuals from contact zones, we follow the current view that *pitmani* is a subspecies of *P. prexaspes* as in its sister species *P. fuscus*, where abundant polytypic phenotypes are found with low genetic divergence (Fig. 6).

The Hainan population, *bowringi*, most resembles *P. p. pitmani* in appearance as some authors pointed out (Haugum & Collins 1987; Joicey & Talbot 1924) (Figs 1–4), although this taxon was established based on comparisons with *P. p. prexaspes*, *P. p. dayacus* and *P. p. andamanicus*. Even though no significant differences were detected in male copulatory apparatus, it was found that the Hainan representative can be externally separated from *P. p. pitmani* by several interesting characteristics, such as the more rounded hindwing spots placed closer to the cell (Prout 1919; Smart 1975; D’Abrera 1982; Gu & Chen 1997; Osada *et al.* 1999; Kimura *et al.* 2011; Sheela *et al.* 2019; Inayoshi 2024) (Figs 1–4). Furthermore, the independence of *bowringi* is also supported by the molecular evidence, where the Hainan population forms a monophyletic clade sister to that of *P. p. prexaspes* and *P. p. pitmani* (Fig. 6).

In summary, the Hainan representative is distinct from all the known subspecies of *P. prexaspes* based on our morphological and molecular study. Under the aforementioned premise that *pitmani* and *prexaspes* are the same species, *bowringi* should also be considered conspecific with *prexaspes*. Therefore, we continue to treat *bowringi* and *P. prexaspes* as a single entity, as traditionally arranged by Hancock (1992).

***Papilio prexaspes bowringi* Prout, 1919 普瑞凤蝶海南亚种**

Figs 1, 3–6

*Papilio fuscus bowringi* Prout, 1919: 129; TL: ‘Yülinkang, Hainan’ [Yulingang/榆林港].*Papilio hipponous bowringi*: Joicey & Talbot (1924): 515 + 519; Gu & Chen (1997): 56, fig. 23 for ♂ [reproduced by Zhou *et al* (2022)]; Gu (2002): 686.*Papilio pitmani* ssp.: Haugum & Collins (1987): 207.*Princeps prexaspes bowringi*: Hancock (1992): 4 + 7.**Material:** 4 ♂♂: 20.VII.2024, W.Y. Li leg. (CZL; PB1); 11.VII.2024, W.Y. Li leg. (CZL; PB2); 14.VII.2024, Z. Liu leg. (CZL; PB3); 2.VIII.2024, W.Y. Li leg. (CZL; PB4). 1 ♀: 25.VII.2024, W.Y. Li leg. (CZL; PB5). All specimens were collected at Daguangba Reservoir, Dongfang, Hainan, China, ca. 400 m.**Diagnosis.** This subspecies can be distinguished from all other subspecies by (Fig. 4):

(1) Distal edge of hindwing white spots in spaces 5 and 6 are rounded, not concave.

(2) Hindwing upperside bands from spaces 1 to 3 are complete as in ssp. *pitmani* but degenerate in ssp. *duboisii* or absent in Malayan *prexaspes*-groupAdditionally, it can be separated from ssp. *pitmani* by (Fig. 4):

(3) Hindwing white bands are closer to the cell.

(4) Submarginal lunules on the male hindwing underside are less developed.

**FIGURE 1.** Habitus of *Papilio prexaspes bowringi* from Hainan, China.

**Variation.** (a) Sizes: the male PB4 is apparently larger, even slightly exceeding the female in size. (b) Tail shapes: specimen PB3 bears the narrowest tails, individual variation can also occur in other congeners (Haugum & Collins 1987). (c) White markings: hindwing upperside bands vary from weakly developed (PB1, 3), normal (PB2) to well-present (PB4).

**Distribution.** Endemic to Hainan Is., China (Fig. 5).

**Phenology.** Unclear, may be bivoltine with two known generations. The first known brood is from May to July, and the second brood is in October (H Huang pers. comm.). Probably there is also a brood in late February and March as in ssp. *pitmani*, but this needs future confirmation.

**Remarks.** (1) This subspecies of *P. prexaspes* superficially resembles sympatric *P. polytes*, but can be identified by the shapes of hindwing markings and the absence of the white marginal patches on the forewing, etc. (Fig. 4). (2) A specimen identified as ‘*pitmani*’ was illustrated in Jiang *et al.* (2001) from Fujian, E. China and, judging from the external features, it probably represents an aberration of *P. polytes*.



**FIGURE 2.** Habitus of *Papilio prexaspes*, all other subspecies from Indochina to Malaysia.

● Discussion

Due to minimal differences in appearance, Cotton & Racheli (2006) synonymized ssp. *intricatus* Monastyrskii & Devyatkin, 2003 [TL: Huu Lien, N. Vietnam] with ssp. *duboisi*, concluding that no barriers to genetic exchange exist between the two populations. On the contrary, considering the great distance between N. and S. Vietnam, a region known to foster subspecific differentiation, and the limited material, Inayoshi (2024) temporarily retained the independence of ssp. *intricatus*. Notably, subspecies *duboisi* was described from ‘Thado, Annam’, a locality once clarified by Hancock (1983a, 1985) in Vinh Province. However, according to investigations of the second author, the correct location of Thado is Ta Do, Nghe An Province, on the border with Laos and not too far from the type locality of ssp. *intricatus* (Fig. 5). Therefore, given the geographic proximity of type localities and the lack of superficial divergence, we concur with Cotton & Racheli (2006) in treating all Vietnamese populations as the same taxon, *duboisi*.

All subspecies of *Papilio prexaspes* can be safely divided into two groups zoogeographically and morphologically, the Indo-Chinese *pitmani*-group (*pitmani* + *duboisi*) and Malayan *prexaspes*-group (*prexaspes* + *andamanicus* + *dayacus*). As previously noted, the presence of intermediate individuals in the contact zone between the two groups provides compelling evidence for their conspecific status. While the type locality of *duboisi* is in E. Indochina, Hancock (1992) observed that this subspecies appears to serve as a transitional form, bridging the morphological gap between ssp. *pitmani* to *prexaspes*-group. Although geographic distribution might suggest placing the Hainan *bowringi* in the *pitmani*-group, phylogenetic analyses based on *COI* and *EF-1a* did not support this classification since *bowringi* and *pitmani* do not share a common ancestor that is sister to *prexaspes*-group (Fig. 6). Instead, the Hainan population tends to cluster with *prexaspes*-group rather than with *pitmani* (Fig. 6). Thus, a comprehensive phylogeny incorporating all *P. prexaspes* subspecies is required to elucidate the evolutionary history of the Hainan population.

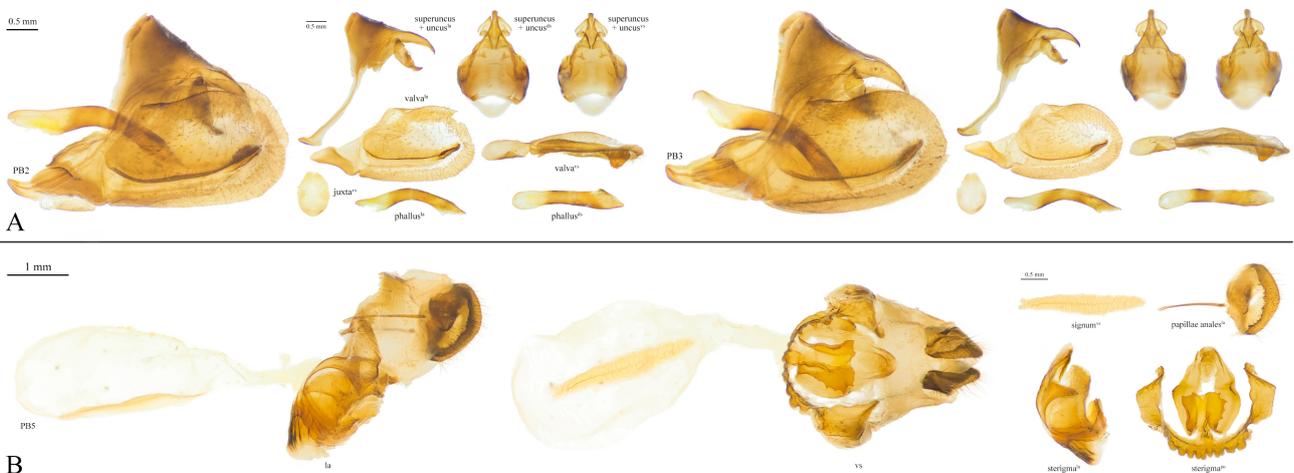


FIGURE 3. Genitalia of *Papilio prexaspes bowringi* A Male genitalia including 8th segment B Female genitalia. la = lateral view, ds = dorsal view, vs = ventral view, po = posterior view.

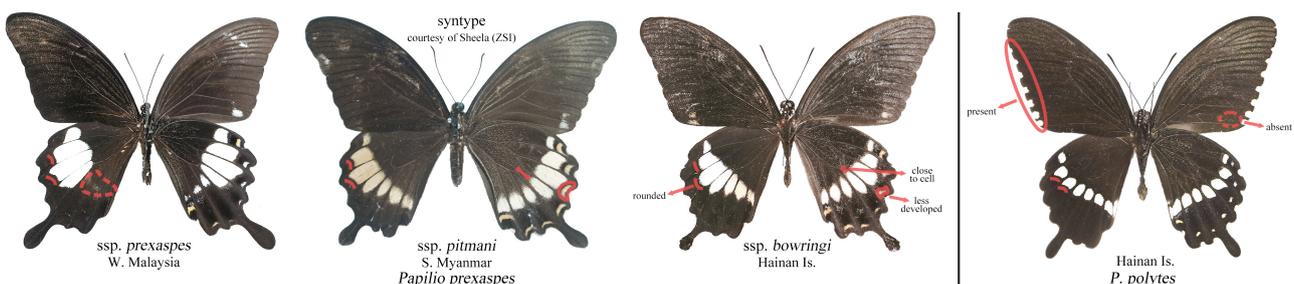
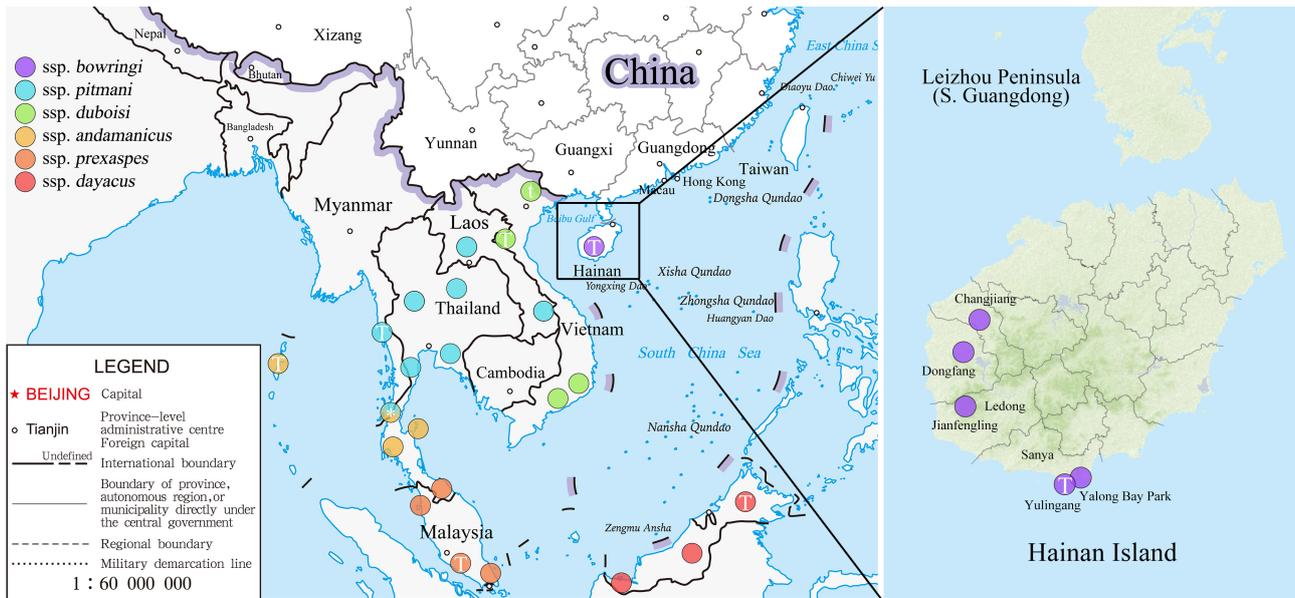


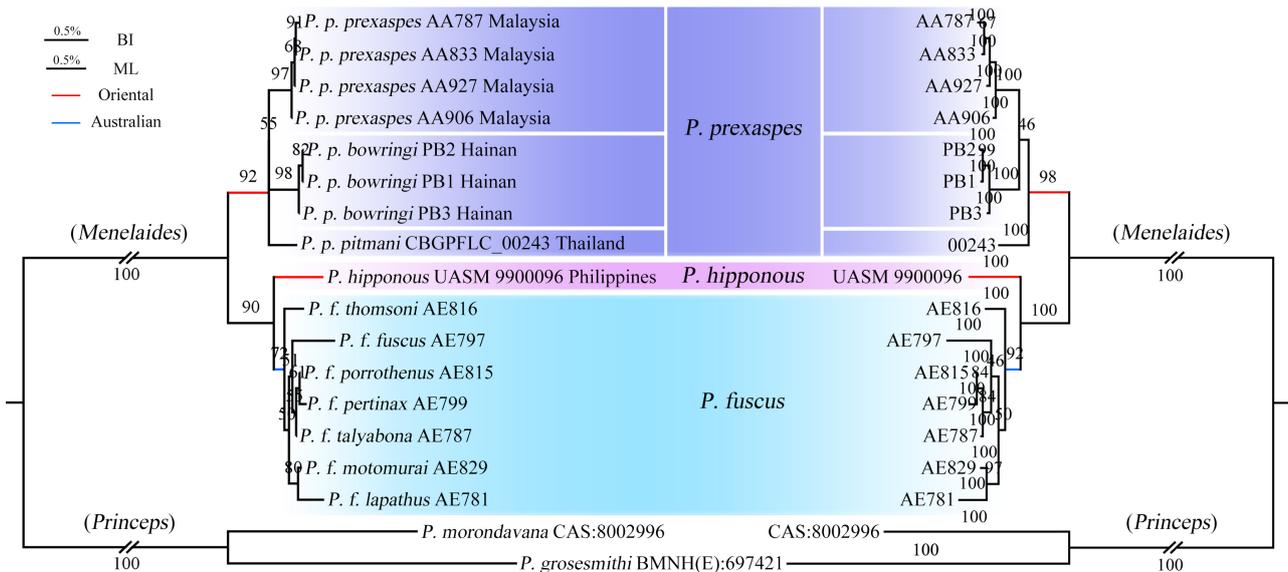
FIGURE 4. Diagnosis of *Papilio prexaspes bowringi*.



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**FIGURE 5.** Distributional map of *Papilio prexaspes*. T and t = type locality of subspecies accepted and synonymized respectively, \* = intermediate individual. Source from references in Material and methods.



**FIGURE 6.** Phylogenetic tree of *Papilio prexaspes* inferred from ML (left) and BI (right) analysis of *COI* and *EF-1a*. Mainly modified from Joshi & Kunte (2022).

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**TABLE 1.** Voucher information and GenBank accession numbers for the *Papilio* specimens in this study.

Taxon	Locality	Voucher Number	Accession Number		Reference
			<i>COI</i>	<i>EF-1<math>\alpha</math></i>	
<i>P. prexaspes bowringi</i>	China	PB1	PQ213161	PQ213863	
<i>P. p. bowringi</i>	China	PB2	PQ213159	PQ213861	The present study
<i>P. p. bowringi</i>	China	PB3	PQ213160	PQ213862	
<i>P. p. prexaspes</i>	—	AA787	<u>KF226576</u> KX557502	KX557925	
<i>P. p. prexaspes</i>	—	AA833	<u>KF226576</u> KX557512	KX557937	
<i>P. p. prexaspes</i>	—	AA906	<u>KF226576</u> KX557549	KX557971	
<i>P. p. prexaspes</i>	—	AA927	<u>KF226576</u> KX557560	—	(Wilson <i>et al.</i> 2013; Joshi & Kunte 2022)
<i>P. fuscus fuscus</i>	—	AE797	KX557613	KX558034	
<i>P. f. pertinax</i>	—	AE799	KX557615	KX558036	
<i>P. f. talyabona</i>	—	AE787	KX558025	KX557604	
<i>P. f. porrothenus</i>	—	AE815	KX557630	KX558050	
<i>P. f. lapathus</i>	—	AE781	KX557598	KX558019	
<i>P. f. motomurai</i>	—	AE829	KX557644	KX558064	
<i>P. f. thomsoni</i>	—	AE816	KX557631	KX558051	
<i>P. p. pitmani</i>	Thailand	CBGPFLC_00243	JF681030	JF681010	(Condamine <i>et al.</i> 2012)
<i>P. hipponous</i>	Philippines	UASM 9900096	AY457576	AY457620	(Zakharov <i>et al.</i> 2004a)
<i>P. morondavana</i>	Madagascar	CAS:8002996	AY569094	AY569098	(Zakharov <i>et al.</i> 2004b)
<i>P. grosesmithi</i>	Madagascar	BMNH(E):697421	AY569090	AY569102	

The underlined accession numbers represent the sequences belonging to different vouchers, which are integrated with the one in the same row since they are of the same taxon.

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