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Pteris caudatipinna (Pteridaceae), a new species from Sabah, Borneo, with a taxonomic reassessment of *P. flava* and *P. glaucovirens*

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ABSTRACT: *Pteris caudatipinna* Y.S.Chao is newly described from Sabah, Borneo, formerly misidentified as *Pteris flava* Goldm. This new species can be distinguished by its free and forked veins, whose veins show an incompletely triangular pattern while remaining free. Phylogenetic analyses based on plastid markers further support the separation of *P. caudatipinna* from *P. flava*. To clarify the application of two historically confused Philippine names, lectotypes are designated here for *P. flava* and *P. glaucovirens* Goldm. Examination of their original material further indicates that these two species are morphologically distinct. Morphologically, the new species is similar to the Philippine taxa with long-caudate pinnae, but can be readily distinguished by having only one pair of basiscopic secondary pinnae (vs. 2–3 pairs) and sterile pinnules with rounded apices (vs. acute or obtuse). The morphology and distribution of the new species are documented, and a comparative table is provided. These findings highlight the floristic affinity between the fern floras of Borneo and the Philippines.

KEY WORDS: Ferns, lectotypification, new species, phylogeny, *Pteris*, Sabah, taxonomy.

INTRODUCTION

Pteris is one of the largest genera in Pteridaceae, comprising approximately 380 species (Borsch *et al.*, 2020) and exhibiting considerable morphological diversity. Continuous taxonomic efforts have revealed numerous new species, especially in tropical Asia (Chao *et al.*, 2017, 2021, 2023). During field investigations in Sabah (Borneo, Malaysia), a plant (Fig. 1) was initially identified as "*Pteris flava* Goldm." However, comparison with the type specimen of *P. flava* from the Philippines (Fig. 2) revealed clear morphological differences. In *P. flava*, adjacent vein branches approach one another but remain free, producing a characteristic triangular, areole-like pattern (Fig. 2B), whereas the Sabah specimens have freely forked veins without such a pattern. In addition, the pinnae of *P. flava* are deeply pinnatifid, with the incisions terminating ca. 2 mm from the costa, whereas those of the Sabah specimens are completely divided to the costa. Given that venation and lamina dissection serve as important diagnostic traits for species delimitation in *Pteris* (Chao *et al.*, 2014), these morphological differences prompted us to re-evaluate the taxonomic identity of the Sabah specimens.

These Sabah specimens also show similarities with *P. borneensis* Y.S.Chao (Chao *et al.*, 2017), particularly in their rounded pinnule apices. However, our new collection differs in having a brown to reddish stipe, whereas *P. borneensis* has a red to dark red stipe. Since a dark red stipe is a key characteristic of sect. *Hypsopodium* (Chao *et al.*, 2023), the specimens do not belong to this section; instead, it could be a member of *Pteris*: subg. *Campteria* sect. *Campteria*. We observed that the long-caudate pinnae of the plant resemble those of several Philippine species in sect. *Campteria*, such as *P. glaucovirens* Goldm. (Copeland, 1958).

The taxonomic interpretation of *Pteris flava* is complicated by its historical treatment in relation to *P. glaucovirens* Goldm. Both names were published by Goldmann (1843) from material collected in Manila, Philippines, but neither name was originally typified. Copeland (1958) subsequently treated *P. flava* as conspecific with *P. glaucovirens*, considering their differences to represent only individual variation. Therefore, in addition to describing the Sabah material as a new species, we re-evaluate the application of the names *P. flava* and *P. glaucovirens* and designate lectotypes for both species.

To clarify the taxonomic status of these specimens, we performed detailed morphological and phylogenetic analyses. We also examined the original material of *P. flava* and *P. glaucovirens* to clarify the application of these two historically confused names and to establish their nomenclatural types.

MATERIALS AND METHODS

Specimens were collected from the Kinabalu National Park and Mount Trus Madi, Sabah, Malaysia. Specimens were deposited at the Sandakan Herbarium (SAN) of the Forest Research Centre, Sabah Forestry Department, Sabah National Park Herbarium (SNP), and the Taiwan Forestry Research Institute (TAIF). To clarify the morphological variation and distribution of the putative

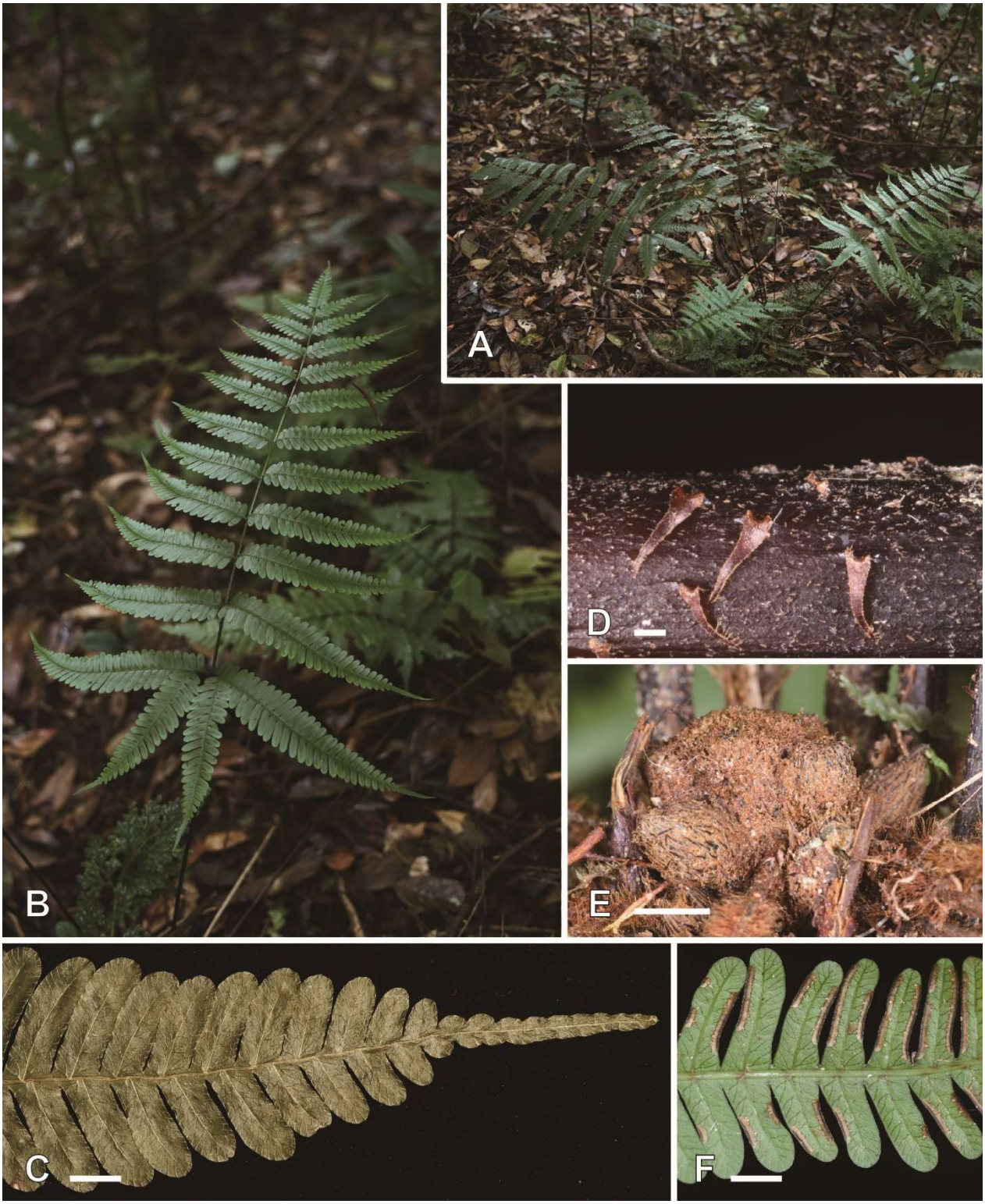

Fig. 1. Morphology of ***Pteris caudatipinna*** Y.S.Chao sp. nov. **A.** Habitat in Kinabalu National Park, Sabah, Malaysia. **B.** Sterile frond, with pinnae gradually narrowing distally and apices long-caudate. **C.** Adaxial surface of pinna, showing pinnules with rounded apices and forked veins. **D.** Brown scales on stipe. **E.** Rhizome with scaly buds. **F.** Abaxial surface of pinna. Scale bars: C, E, F = 5 mm; D = 1 mm. Photographs by Y.-S. Chao. All photographs were taken from the holotype, *Y.-S. Chao 3416*.

Fig. 2. Holotype of ***Pteris flava*** Goldm. from Manila, Philippines (B 20 0127555). **A.** Holotype specimen. **B.** Pinna showing veins nearly triangular costal areoles (indicated by arrows). Scale bar = 5 mm.

new species, we further examined the type material and additional specimens of *Pteris* species that resemble it, including *P. flava*, *P. dataensis* Copel., *P. glaucovirens*, and *P. pedicellata* Copel., deposited in the herbaria B, BRIT, K, MICH, SAN, SNP, S, TAIF, and US.

For the phylogenetic analysis, we sampled 39 *Pteris* species, focusing on subclades of sect. *Campteria* from previous studies (Chao *et al.*, 2014; Chao and Huang, 2018). Additionally, we included two bipinnatifid species with rounded pinnule apices, *P. bella* Tagawa and *P. borneensis*, from sect. *Hypsopodium*. To enhance our analysis, we also included some species from sect. *Cadierii*, sect. *Excelsae*, sect. *Creticae* and sect. *Tripedipteris*. All of the aforementioned taxa are classified under subgenus *Campteria*, given the presence of two subgenera within the genus *Pteris*. Species from *Pteris subg. Pteris* were chosen as outgroups, represented by *P. longifolia* L. and *P. vittata* L.

Following a modified cetyltrimethylammonium bromide (CTAB) method (Doyle and Doyle, 1990; Allen *et al.*, 2006), we extracted the total genomic DNA from the silica-dried leaves. Two plastid genes, *rbcL* and *matK*, were amplified with the same PCR primers as Chao *et al.* (2014). For this taxon, we sequenced three individuals collected from different localities in Sabah. For each of the Philippine relatives and relevant outgroups, one individual per species was sequenced. The gained sequences were aligned with MUSCLE (Edgar, 2004) in BioEdit 7.1.3 (Hall, 1999).

We used IQ-TREE v. 2.2.0 (Nguyen *et al.*, 2015; Trifinopoulos *et al.*, 2016; Minh *et al.*, 2020) to perform Maximum Likelihood (ML) analysis. The *rbcL* alignment was partitioned by first, second, and third codon positions (partitions 1–3), and *matK* was partitioned in the same manner (partitions 4–6). The best-fit substitution models and partitioning scheme were selected via PartitionFinder (Lanfear *et al*., 2017) and ModelFinder (Kalyaanamoorthy *et al.*, 2017) based on the Bayesian Information Criterion (BIC) (Chernomor *et al.*, 2016). Node supports were calculated by performing 10,000 replicates of both the SH-like approximate likelihood-ratio test (SH-aLRT; Guindon *et al.*, 2010) and the ultrafast bootstrap replicates (UFBoot; Hoang *et al.*, 2018). The resulting topologies were visualized using FigTree v. 1.4.4. (Rambaut, 2018).

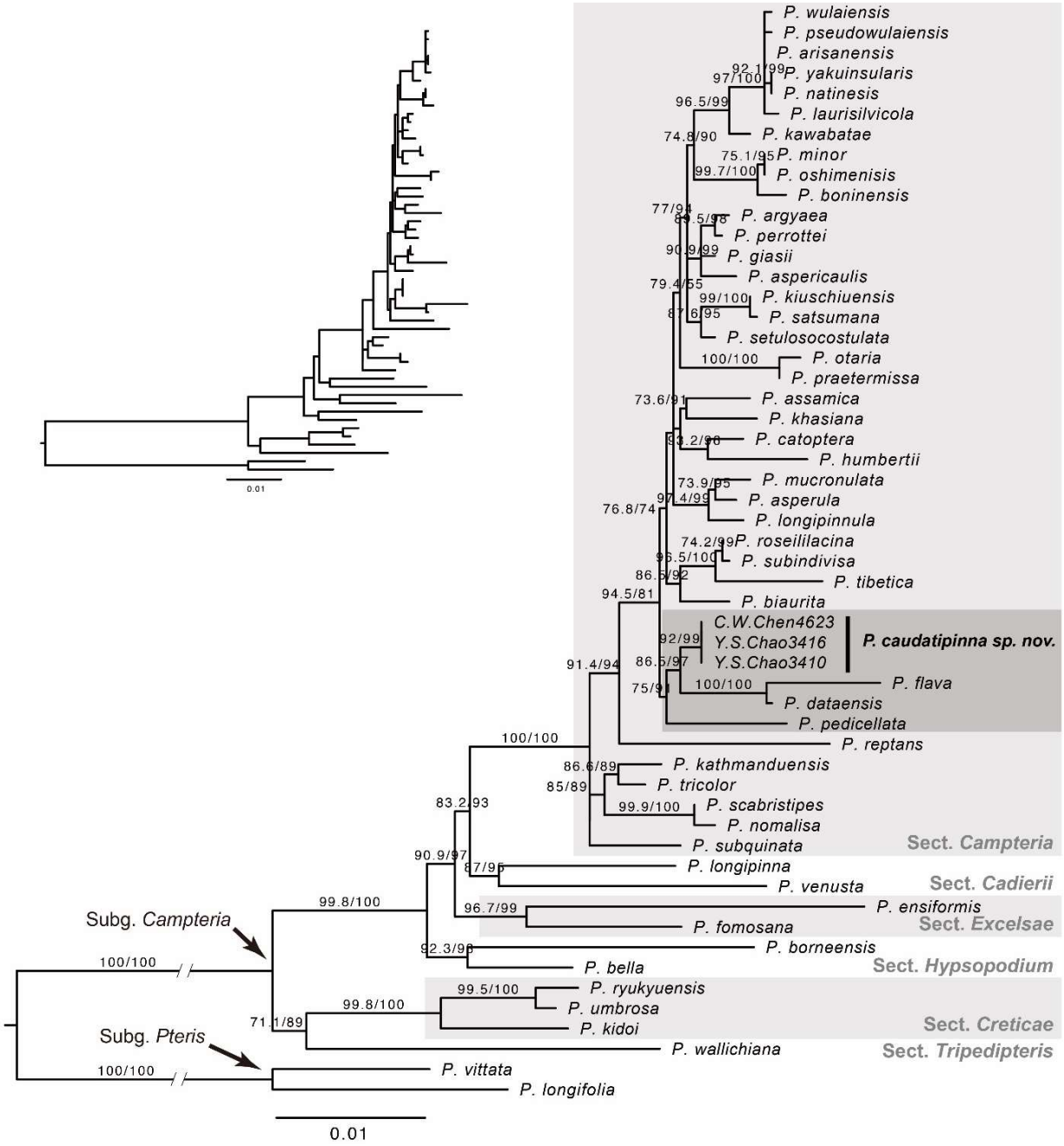

Fig. 3. Maximum-likelihood (ML) phylogenetic tree showing the position of ***Pteris caudatipinna*** Y.S.Chao. Support values (SH-aLRT/UFBoot) are shown above each branch. Values below 50% are not shown.

Table 1. Statistics for the DNA sequence alignments for datasets comprising all samples and one representative sample per species. Best-fit model according to BIC.

Dataset	Aligned length (bp)	Codon position and selected model	Parsimony informative sites (bp)
rbcL	1,298	1: TPM2u+F+I+G4	16 (3.76%)
		2: TPM2+I	8 (1.88%)
		3: K3Pu+F+R2	83 (19.48%)
matK	810	4: K3Pu+F+R2	73 (24.17%)
		5: K3Pu+F+G4	68 (22.52%)
		6: K3Pu+F+G4	80 (26.49%)

RESULTS AND DISCUSSION

The ML tree and the dataset are shown in Fig. 3 and Table 1, with voucher information detailed in Table S1. The resulting topology aligns with previous studies (Chao *et al.*, 2014; Zhang *et al.*, 2015). Phylogenetic analyses using plastid markers, *rbcL* and *matK*, consistently place the plant within *Pteris* sect. *Campteria*, where it forms a strongly supported subclade (SH-aLRT/UFBoot = 75/91) with *P. dataensis*, *P. flava*, and *P. pedicellata*. The

phylogenetic position also clearly separates this plant from those with rounded pinnule apices (*P. borneensis* in sect. *Hypsopodium*). Thus, phylogenetic analyses confirm that this plant occupies a distinct phylogenetic position.

Goldmann (1843) described *Pteris flava* and *P. glaucovirens* from Manila, and recognized them as distinct species. While he noted their close similarity, he distinguished *P. flava* from *P. glaucovirens* mainly by the sori, which nearly meet at the segment apices in *P. flava* but terminate before the apices in *P. glaucovirens*. Goldmann listed only "Manila" as locality and did not designate type specimens. His study was based on specimens collected by F.J.F. Meyen during his 1830–1832 circumnavigation, and the Berlin Herbarium (B) acquired Meyen's main set (Schwartsburd *et al.*, 2025).

Our examination of original material housed at B and S clarifies the application of these names and allows us to designate lectotypes for both species. In addition to the soral differences noted by Goldmann, the type material shows further morphological distinctions: in *P. flava* (Fig. 2), adjacent vein branches approach one another without fusing, forming a characteristic triangular, areole-like pattern, and the sterile pinnules or segments have obtuse apices, whereas in *P. glaucovirens* (Fig. 4) the veins are freely forked without forming such a pattern and the sterile pinnules or segments are mostly acute. These differences in the original material contradict the synonymy proposed by Copeland (1958), supporting our recognition of *P. flava* and *P. glaucovirens* as distinct species.

We highlight the key morphological differences between the new species and its closest relatives in Table 2. The three species, *P. dataensis*, *P. glaucovirens*, and *P. pedicellata*, share long-caudate pinna apices, 2–3 pairs of basiscopic secondary pinnae on the basal pinnae, 10–16 pairs of lateral pinnae, and sterile pinnules with acute or obtuse apices. In contrast, the new species is unique in having only one pair of basiscopic secondary pinnae on the basal pinnae and rounded pinnule apices.

The venation pattern of *P. flava*, with adjacent vein branches approaching one another but remaining free, thereby producing a triangular, areole-like pattern (Fig. 2), resembles that of *P. arisanensis* Tagawa. *Pteris arisanensis* has a complicated evolutionary relationship with *P. biaurita* L. (Chao *et al.*, 2022). In our phylogenetic analyses, the two species are phylogenetically distant from the putative new species (Fig. 3).

The putative new species is endemic to Sabah, while the other members of the subclade are restricted to the Philippines (Copeland, 1958). Borneo and the Philippines share notable biogeographical connections in plants, such as *Tetrastigma loheri* Gagnep. (Vitaceae) (Obico *et al.*, 2021), genus *Burbidgea* Hook. f. (Zingiberaceae) (Mazo *et al.*, 2022a), and *Sulettaria longituba* (Ridl.) A.D. Poulsen & Mathisen (Zingiberaceae) (Mazo *et al.*, 2022b). Dispersal events were inferred to shape the floras, e.g. *Begonia* sect. *Baryandra* colonized via long-distance dispersal from western Malesia (which includes Borneo) to the Philippines during the late Miocene and the Plio-Pleistocene (Hughes *et al.*, 2015). Despite overlapping distributions, both regions have strong endemism. For example, *Nepenthes* (Nepenthaceae) is highly diverse in the Philippines, where some species are shared with Borneo, but many *Nepenthes* species are unique to each region, reflecting localized speciation (Gronemeyer *et al.*, 2014; Amoroso *et al.*, 2017). In this study, the distribution pattern observed in *P. caudatipinna* is consistent with this broader biogeographical relationship between Borneo and the Philippines, while also reflecting the high level of regional endemism in both areas.

The combination of phylogenetic isolation and unique morphological traits supports recognition of this plant as a distinct species, *Pteris caudatipinna* Y.S.Chao. We provide a taxonomic description below.

Fig. 4. Lectotype of ***Pteris glaucovirens*** Goldm. (B 20 0146843).

Table 2. Comparison of diagnostic morphological and distributional characters among ***Pteris caudatipinna*** sp. nov. and four morphologically similar species. Traits distinguishing each species from the others are shown in bold.

Character/species	*P. caudatipinna*	*P. flava*	*P. dataensis*	*P. glaucovirens*	*P. pedicellata*
Stipe	**Brown to reddish**	Stramineous to brown	Stramineous to brown	Stramineous to brown	Stramineous to brown
Number of lateral pinnae	7–11 pairs	9–12 pairs	Up to 13 pairs	7–10 pairs	9–14 pairs
Pinna shape	Widest at base	Widest at base	**Narrowed at base**	Widest at base	Widest at base
Pinna stalk	**Sessile**	Sessile to 3 mm	Sessile	2 mm	2–3 mm
Pinna width	2–3 cm	1.5–2.5 cm	ca. 2 cm	to 5 cm	1.5–3.0 cm
Basiscopic secondary pinnae on basal pinnae	**One pair**	**1 or 2 pairs**	2 or 3 pairs	2 or 3 pairs	2 or 3 pairs
Pinna dissection	**Completely divided to the costa**	Deeply pinnatifid, incisions terminating ca. 2 mm from the costa	Completely divided to the costa	Completely divided to the costa	Completely divided to the costa
Angle of pinnules to the costa	**81–90°**	71–80°	71–80°	71–80°	71–80°
Pinnule shape	**Oblong**	Falcate	Falcate	Falcate	Falcate
Sterile pinnule apex	**Rounded**	Obtuse	Obtuse	**Acute**	Obtuse
Venation pattern	Freely forked	**Vein branches approaching one another but remaining free forming a triangular, areole-like pattern**	Freely forked	Freely forked	Freely forked
Distribution	Sabah	Philippines	Philippines	Philippines	Philippines

TAXONOMIC TREATMENT

Pteris caudatipinna Y.S.Chao, ***sp. nov.*** **Figs. 1A–F**

Type: **MALAYSIA.** Sabah: Kota Belud, Kinabalu Park Substation Sayap, trail to Mt. Minodtuhan, 1800 m, 1 May 2023, *Y.S. Chao 3416* (holotype: SNP!; isotypes: SAN!, TAIF!).

Diagnosis: Similar to *P. dataensis*, *P. glaucovirens,* and *P. pedicellata* but distinguished by a single pair of basiscopic secondary pinnae on the basal pinnae (vs. 2–3 pairs), rounded sterile pinnule apices (vs. acute or obtuse), and restriction to Sabah, Borneo. The new species was previously misidentified as *P. flava*, but differs in having free and forked veins (vs. incompletely triangular veins in *P. flava*).

Description: Terrestrial. ***Rhizomes*** short-creeping, covered with concolorous, brown scales. ***Fronds*** clustered. Stipes 20–55 cm long, brown to reddish, smooth, bearing scales. Laminae lanceolate, 30–60 cm long, 15–25 cm wide, bipinnatifid, texture chartaceous; lateral pinnae 7–11 pairs, nearly sessile or the lowest stalked; basal pinnae bearing one long basiscopic secondary pinna; pinnae oblong, 2–3 cm wide, pectinate, with apices gradually tapering and caudate; pinnules oriented at an angle of 81–90° to the costa; sterile pinnules oblong, 3–5 mm wide, rounded apices; fertile pinnules falcate or oblong, 3 mm wide, apices obtuse or rounded; veins forked, free. ***Sori*** linear, along margin of pinnules; pseudoindusia entire.

Distribution and Habitat: Endemic to Sabah, Malaysia (Borneo), where it has been recorded from Mount Trus Madi, Mount Kinabalu, and the Sayap Substation area of Kinabalu Park (Kota Belud). It occurs in shaded forest understory, along montane trails, at elevations of ca. 1700–2200 m.

Etymology: The specific epithet "caudatipinna" is derived from 'caudate' (tail-like) and 'pinna'. It refers to the pinnae with apices gradually extended into a caudate form.

Specimens examined: MALAYSIA. Sabah: Mount Trus Madi, near Resthouse, 10 Apr 2015, *Y.-S. Chao 2377, 2378, 2388* (SAN, SNP, TAIF); Kota Belud, Kinabalu Park, Sayap Substation, trail to Mt. Minodtuhan, 1200–2300 m, 1 May 2023, *Y.-S. Chao 3393, 3395, 3410, 3411* (SAN, SNP, TAIF); Mt. Kinabalu, Summit Trail between Timpohon Gate and main resthouse, 4 Mar 2016, *C.-W. Chen Wade4623* (SAN, SNP, TAIF); Mt. Kinabalu, Cascades Trail, ca. 1700 m, 8 Nov 1980, *B.S. Parris & J.P. Croxall 9096* (K); Kamborangah, ca. 2134 m, 17 Nov 1931, *C. Christensen 25521* (K).

Pteris flava Goldm. in Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 19(Suppl. 1): 457. 1843 – ***Lectotype*** (designated here): **PHILIPPINES.** Manila, *F.J.F. Meyen s.n.* (B 20 0127555 [image!]; probable isolectotype: S No. S-P-5933 [image!]). **Fig. 2**

Description: Stipes stramineous to brown. Laminae lanceolate, bipinnatifid; lateral pinnae nearly sessile or the lowest stalked, oblong to narrowly lanceolate, pectinate, deeply pinnatifid, with incisions terminating ca. 2 mm from the costa, apices gradually tapering and caudate; basal pinnae bearing 1–2 pairs of basiscopic secondary pinnae; pinnules oblong, with obtuse apices; veins forked, with adjacent branches approaching one another but remaining free, producing a triangular, areole-like pattern. Sori linear, nearly confluent at the apices of the segments; pseudoindusia entire.

Note: We located original material at B and S, both

bearing labels reading "*Pteris flava* n. sp., Manila, Meyen". The specimen at B is more complete and is housed in the herbarium that acquired Meyen's main set; we therefore designate B 20 0127555 (Fig. 2) as the lectotype.

Pteris glaucovirens Goldm. in Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 19(Suppl. 1): 457. 1843 – ***Lectotype*** (designated here): **PHILIPPINES.** Manila, *F.J.F. Meyen s.n.* (B 20 0146843 [image!]; isolectotype: B 20 0146844 [image!]). **Fig. 4**

Description: Stipes brown. Laminae lanceolate, bipinnatifid; lateral pinnae with stipe 2–5 mm long, oblong-lanceolate, pectinate, acuminate to long-caudate; basal pinnae bearing 2–3 pairs of basiscopic secondary pinnae; pinnules or segments oblong, mostly acute at the apex in the type material; veins forked and free, without forming a triangular, areole-like pattern. Sori linear and continuous, terminating before the apices of the segments.

***Note*:** Two specimens at B bearing early labels reading "*Pteris glaucovirens* Goldmann, Manila, Meyen" were both regarded as original material. B 20 0146843 (Fig. 4) is the more complete specimen and includes a larger portion of the lamina and basal pinnae; we therefore designate it as the lectotype.

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Supplementary materials are available from the journal website