



Aristolochia argilophila (Piperaleae: Aristolochiaceae), a new species from Brunei Darussalam, with notes on the taxa *Aristolochia foveolata* Merr. and *Aristolochia transtillifera* Ding Hou

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Summary. *Aristolochia foveolata* is currently regarded as a variable species distributed across Maritime Southeast Asia. Through field observations, geometric morphometric analysis, and traditional morphological examination, we propose that specimens previously identified as *A. foveolata* from Borneo belong instead to *Aristolochia papillifolia*, *Aristolochia transtillifera*, and a taxon we describe and illustrate here as a new species, *Aristolochia argilophila*, from Brunei Darussalam. A detailed comparison of *A. argilophila* with its morphologically closest relatives is provided, comments on taxonomy and geographic distribution, as well as a preliminary assessment of the conservation status. Based on the generated data we further propose to exclude *A. foveolata* from the Flora of Borneo, and complement the description of *A. transtillifera*, of which flowers had not been described to date. We discuss the extraordinary vegetative plasticity of the taxa in affinity to *A. papillifolia* on Borneo, unveiling present inconsistencies in current species circumscriptions and providing a first revision of these scarcely known entities, which highlights the importance of floral structures for accurate species delimitation in *Aristolochia*.

Key Words. Aristolochioideae, Borneo, Flora, morphology, morphometrics, taxonomy.

Introduction

The genus *Aristolochia*, comprising approximately 550 species across five continents, exhibits remarkable diversity especially in tropical regions (Phupathanaphong 2006; Buchwalder *et al.* 2014; González & Pabón-Mora 2018; Zhu *et al.* 2019; Jiménez & Blanco 2020; POWO 2025). The current taxonomy recognises all three subgenera for Borneo: *Siphisia* (Raf.) Duch. (Brunei Darussalam, Sarawak), *Pararistolochia* (Hutch. & Dalziel) O.C. Schmidt (Kalimantan), and *Aristolochia* L. (Malaysian Borneo, Indonesian Borneo, and Brunei Darussalam), which includes section *Diplolobus* (Duch.) Duch., and both subsections *Podanthemum* (Klotzsch) Duch. and *Euaristolochia* (Klotzsch) Schmidt (González & Stevenson 2002; Hou 1983a, b; Yao 2015). The genus has been a matter of revision twice in Borneo and Malaysia by Hou (1983a, b) and Yao (2015), respectively. Most Bornean species are currently circumscribed with broad distribution ranges but known from relatively few collections only. The majority of large *Aristolochia* lianas with coriaceous leaves and corky stems in Borneo, Sumatra, and Peninsular Malaysia has been classified as *A. foveolata* in subsection *Euaristolochia*, a species originally described

from fruiting material, collected in Luzon, northern part of the Philippines (Merrill 1918; Hou 1983b; Sutton *et al.* 2021). The type specimen (*M. Ramos* 30370, Luzon, Catanduanes) represents a small, scrambling to twining liana with herbaceous stems and axillary flowers on apical, young shoots. However, specimens attributed to this taxon from Borneo exhibit cauliflorous flowering on corky stems (> 2 years old and/or old bark). Such discrepancies, observed in herbaria, cultivated specimens, and during surveys, necessitate a comprehensive revision of cauliflorous taxa related to *A. papillifolia* Ding Hou in Borneo. Cauliflorous specimens related to *A. papillifolia* (hereafter referred to as the *papillifolia* group) fall under *Aristolochia* section *Diplolobus*, subsection *Euaristolochia* (Duchartre 1854, 1864; Ohi-toma *et al.* 2006; González & Pabón-Mora 2019).

Aristolochia flowers are protogynous; following anthesis the stigma is receptive for about 24 to 48 h followed by pollen release in the subsequent male stage and finally abscission after less than 72 to 96 h (González & Stevenson 2000a, b). Rapid decay in humid environments further complicates taxonomic efforts as the diagnostic flowers are barely encountered

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in the field which likely has been obstructing a clearer view in previous studies (Hou 1983a, b; Yao 2015). The vegetative appearance particularly including the leaf shape is highly plastic, not only within individuals of different species or individuals within a population, but remarkably even within single stems of the same plant. While studying *Aristolochia* specimens in herbaria across Asia, Europe, and the Americas, we identified several taxonomic inconsistencies in specimens from Borneo. Using geometric morphometrics analysis of leaves and flowers, this study focuses on revising the *papillifolia* group of Borneo.

The morphology of flowers, fruits, and seeds are widely referred to as the diagnostic structures in *Aristolochia*, especially to differentiate otherwise vegetatively similar and closely related species and groups of taxa (Blanco 2002; Freitas *et al.* 2020). We stumbled across a hitherto overlooked entity in field studies in Brunei Darussalam that we propose as a new species herein, *A. argilophila* sp. nov. A detailed morphological comparison, corroboration with geometric morphometrics, remarks on closely related taxa, illustration of diagnostic characters, and a preliminary assessment of extinction risk are provided. Additionally, we provide an amended description of *A. transtillifera*, which was previously described without flowers, based on a flowering and fruiting specimen collected from Inobong Substation, Crocker Range Park by J. Yabainus *et al.* KNP 14555 (Hou 1983a).

Materials and Methods

Field surveys were conducted in various forest reserves across Brunei Darussalam and Sabah to assess the occurrence of the relevant *papillifolia* group congeners. A total of 45 herbarium vouchers were studied, comprising 13 specimens of *Aristolochia papillifolia*, 21 of *A. transtillifera*, and 11 of *A. argilophila* sp. nov. These were sourced from the following herbaria (acronyms follow Thiers 2025): A, BORH, BRUN, K, L, SAN, SAR, SNP. Only fully developed leaves and flowers at late pre-anthesis were selected for geometric morphometric analyses to minimise inaccuracies from immature flowers with distorted properties (Frank 2023; Freitas *et al.* 2020, 2024). Each flower was analysed using nine (9) homologous landmarks, while leaves were assessed with eight (8) landmarks (Fig. 1).

The methods for morphometric analysis followed the protocols developed by Freitas *et al.* (2020) using *TpsDig* version 2.31 (Rohlf 2017) and *MorphoJ* version 1.07a (Klingenberg 2011). Canonical Variate Analysis (CVA) was employed to identify morphological variation contributing to the greatest divergence among the three taxa (Fig. 2). A total of 21 flowers and 129

leaves were examined, including 28 leaves and six (6) flowers of *A. papillifolia*, 63 leaves and seven (7) flowers of *A. transtillifera*, and 38 leaves and eight (8) flowers of *A. argilophila*.

ImageJ software was used to measure peduncle and petiole lengths (Schneider *et al.* 2012). Conservation status evaluations adhered to IUCN guidelines (IUCN 2012, 2024), with the GeoCAT tool used to calculate the Area of Occupancy (AOO) and Extent of Occurrence (EOO) for each species (Bachman *et al.* 2011).

Terminology for vegetative and reproductive structures follows Pfeifer (1966) and González (1990).

Results

Geometric Morphometrics

The morphometric analysis of floral traits clearly differentiated the three taxonomic entities. The first two canonical variates (CV1 = 58.9 %, CV2 = 41.1 %) explained a cumulative 100 % of the observed variation in floral shape (Fig. 2A). Key diagnostic features influencing this variation included the orientation and relative shape of the floral structures, namely the limb, tube, and utricle (Fig. 1). Notably, the angle formed by the proximal and distal ends of the limb (landmarks 4 and 6) relative to the tube (landmark 7), referred to hereafter as the limb's inclination angle, proved to be a particularly distinguishing trait, as detailed in Table 1. Even despite the limited sample size, the morphological characteristics evaluated in this study are sufficient to reliably discriminate *Aristolochia argilophila* from the two morphologically closest entities.

In contrast, leaf shape was found to be a comparatively unreliable characteristic for identifying *Aristolochia* species in Borneo at the species level. The analysis did not reveal any distinct separation among species based on this trait, suggesting significant morphological overlap. This was further supported by the results of the canonical variate analysis, where the first two canonical variates (CV1 = 79.6%, CV2 = 20.4%) accounted for all variation but failed to clearly differentiate the species, indicating that leaf shape alone may not be a sufficient diagnostic feature for taxonomic resolution in this group.

Taxonomic Treatment

***Aristolochia argilophila* D. Frank & M.A.M. Andi sp. nov.** Type: Brunei Darussalam. Belait: Liang, Kg Sungai Liang, Bukit Lumut, 55 m, 04°39'18.9"N, 114°28'19.5"E, 14 Sept. 2024 (fl., fr.), D. Frank, Andi M. A. M., S. Jaafar, M. F. Abdullah & A. Pandai 2 (holotype BRUN, isotype SAN). (Figs 3, 4, Map 1).



Fig. 1. Contours of representative late preanthetic flowers (top line) and leaves (bottom line) of the investigated taxa: **A** *Aristolochia transtillifera*. **B** *A. papillifolia*. **C** *A. argilophila*. Homologous points selected as landmarks for geometric morphometrics of late preanthetic flowers (in lateral view) and leaves are shown in red.

<http://www.ipni.org/urn:lsid:ipni.org:names:77379472-1>

Woody liana. *Stems* terete, glabrous when young, with corky bark when mature; internodes 6 – 18 cm long, pseudostipules absent. Broken stems emit a scent similar to orange. *Leaves* marcescent, leaving petiole remnants after decomposing; petiole 4 – 11 cm long. Lamina coriaceous when adult, cordiform-ovate to cordiform-hastate, 8.5 – 21 × 7 – 15 cm, basally cordate with sinus 1 – 3 cm deep, apically acuminate. Adaxial surface glabrous, abaxial surface papillate, venation pedate. *Inflorescences* cymose, 0.5 – 1 cm long, inflorescence internodes 0.1 – 0.3 cm apart, with 1 – 8 flowers, cauliflorous. Petiole 4 – 11 cm long, glabrous.

Bracts ovate, glabrous. *Flowers* protogynous, peduncle plus ovary 2 – 3.2 cm long (at anthesis), glabrous, perigone geniculate. Outer surface glabrous, beige to pale brown or purple. *Utricle* elongated obpyriform, gibbous, 1.5 – 2 × 0.7 – 0.9 cm, inner surface beige, densely covered by short white trichomes with tomentose appearance. Glandular bodies 2, elongated-elliptical in shape (Fig. 3G, upper inlet). *Syrinx* absent. *Tube* cylindriform, 0.5 – 1.2 cm long, inner surface beige, densely covered by white trichomes. *Fauces* round, beige transitioning to dark purple with white trichomes. *Limb* unilabiate, linear, revolute, sometimes curled around itself, 4 – 5 × 0.7 – 1 cm, inclination angle 60 – 80°, glabrous, apex mucronate, brown to

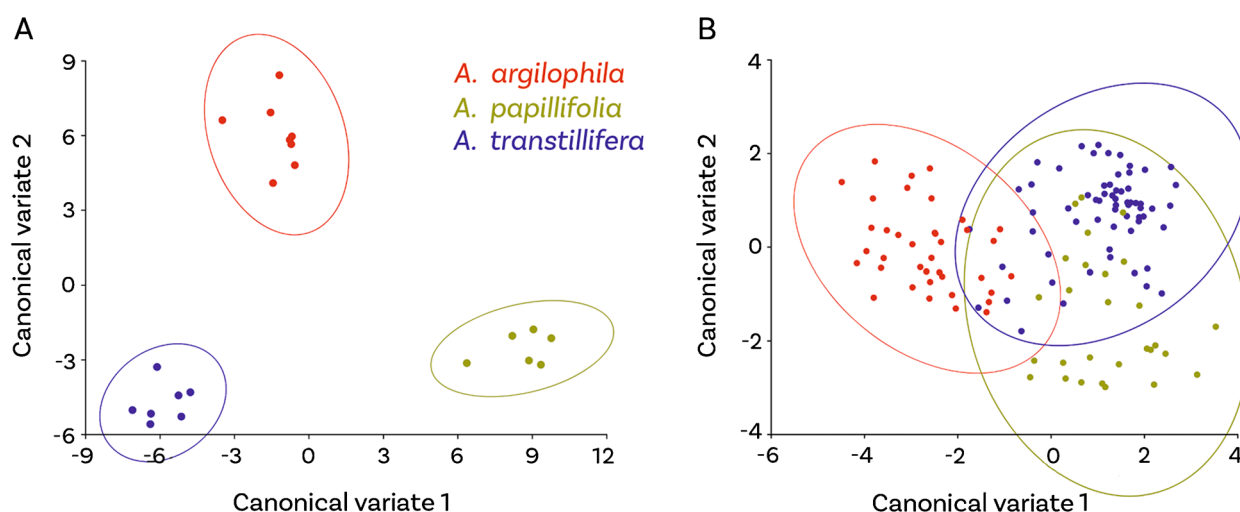


Fig. 2. Canonical Variate Analysis (CVA) of selected landmarks of the three *Aristolochia* entities, coloured by species identity. **A** flowers; **B** leaves.

Table 1. Morphological comparison of *Aristolochia argilophila* with its closest morphological congeners, derived from field observations and vouchered specimens.

	<i>Aristolochia argilophila</i>	<i>Aristolochia transtillifera</i>	<i>Aristolochia papillifolia</i>
Leaf blade [cm]	8.5 – 21 × 7 – 15	11 – 24 × 4 – 11	9 – 23 × 6 – 19
Petiole length [cm]	4 – 11	3.5 – 7	4 – 14
Leaf shape and size	cordiform-ovate to cordiform-hastate, wide sinus	cordiform-elongate to deltoid, wide or absent sinus	cordiform-ovate, wide sinus
Leaf surface - adaxial	glabrous	glabrous	glabrous
Leaf surface - abaxial	papillate	papillate	papillate
Peduncle length [cm]	2 – 3.2	3 – 4.5	2.8 – 3.5
Utricle shape	elongate obpyriform	rounded	rounded
Utricle size [cm]	1.5 – 2 × 0.7 – 0.9	0.6 – 0.8 × 0.5 – 0.7	0.6 – 0.8 × 0.4 – 0.7
Glandular bodies	2, elongated-elliptical	6, round	6, round
Tube size [cm]	0.5 – 1.2	0.8 – 1.5	1.5 – 2.2
Limb size [cm]	4 – 5 × 0.7 – 1	2.5 – 4 × 0.8 – 1.2	3 – 4.5 × 0.8 – 1.5
Limb inclination [°]	60 – 80	80 – 125	25 – 50
Trichomes on limb	dense cover on fauces and proximal part above the fauces	dense cover on fauces and more than half of the limb length	absent
Capsule size [cm]	5 – 6 × 1.5 – 2	3 – 4 × 1 – 1.8	4 – 6 × 1 – 1.8
Seeds	5 – 6 × 3 – 4 mm, obovate	5 – 6 × 3 – 5 mm, triangular to obovate	5 – 6 × 3 – 4 mm, obovate
Distribution	Brunei Darussalam	Brunei Darussalam; Malaysia: Sabah; Philippines: Palawan	Malaysia: Sabah, Sarawak; Indonesia: Kalimantan

dark purple, white trichomes restricted to the proximal part above the fauces (Fig. 3F). *Gynostemium* depressed coroniform, 0.3 – 0.5 × 0.2 – 0.3 cm. Stigmatic lobes 6, beige in colour. Anthers 6, short-oblong, c. 1 mm long. *Fruit* capsules cylindric, 5 – 6 × 1.5 – 2 cm, apex rounded, glabrous, with basal, septicial dehiscence. *Seeds* obovate, 0.5 – 0.6 × 0.3 – 0.4 cm, non-winged, dark brown, abaxial surface papillate, adaxial side with sticky elaiosome present (Fig. 3H).

RECOGNITION. *Aristolochia argilophila* is distinguished from *A. foveolata* by its cauliflorous flowering habit (vs axillary-flowered in *A. foveolata*), the flower shape including the limb length (*A. argilophila*: 4 – 5 cm vs *A. foveolata*: 0.5 – 2 cm) and inclination of the limb (60 – 80° vs 90 – 110° in *A. foveolata*) and the number and shape of glandular bodies (2 ellipsoid glandular bodies, vs 6 round glandular bodies in *A. foveolata*). It differs from *A. papillifolia* and *A. transtillifera* in the



Fig. 3. *Aristolochia argilophila* sp. nov. **A** habit including woody stem; **B** leaves adaxial (left) and abaxial (right); **C** fruit; **D** anthetic flower in lateral view; **E** late preanthetic flower; **F** anthetic flower in frontal view, note the restriction of trichomes to the tube and the fauces; **G** longitudinally dissected anthetic flower, note the magnified glandular body (top inset) and the gynostemium (bottom inset); **H** seed abaxial (left) and adaxial (right). Scale bar: **A** 6 cm; **B**, **C** 5 cm; **D** – **G** 2.5 cm; **H** 1 cm. From the type specimen Frank, Andi, Jaafar, Abdullah & Pandai 2. PHOTOS: DOMINIK FRANK.

limb's trichome coverage of the perianth (trichome coverage restricted to the area above fauces in *A. argilophila* vs absent in *A. papillifolia* and covering more than half of the limb in *A. transtillifera*), the number and shape of glandular bodies (2 ellipsoid glandular bodies in *A. argilophila* vs 6 round glandular bodies in both *A. papillifolia* and *A. transtillifera*), and the limb inclination angle ($60 - 80^\circ$ in *A. argilophila* vs $25 - 50^\circ$ in *A. papillifolia* and $80 - 125^\circ$ in *A. transtillifera*).

DISTRIBUTION. *Aristolochia argilophila* is endemic to Brunei Darussalam, found in the Belait, Brunei-Muara, and Tutong districts. Map 1.

HABITAT. The species is found in lowland forests at elevations up to 170 m above sea level, showing a preference for loamy, clay-rich soils.

SPECIMENS EXAMINED. **BRUNEI DARUSSALAM.** Belait: Labi, Bukit Telingan, 213 m, $04^\circ 22' 39.2''\text{N}$,

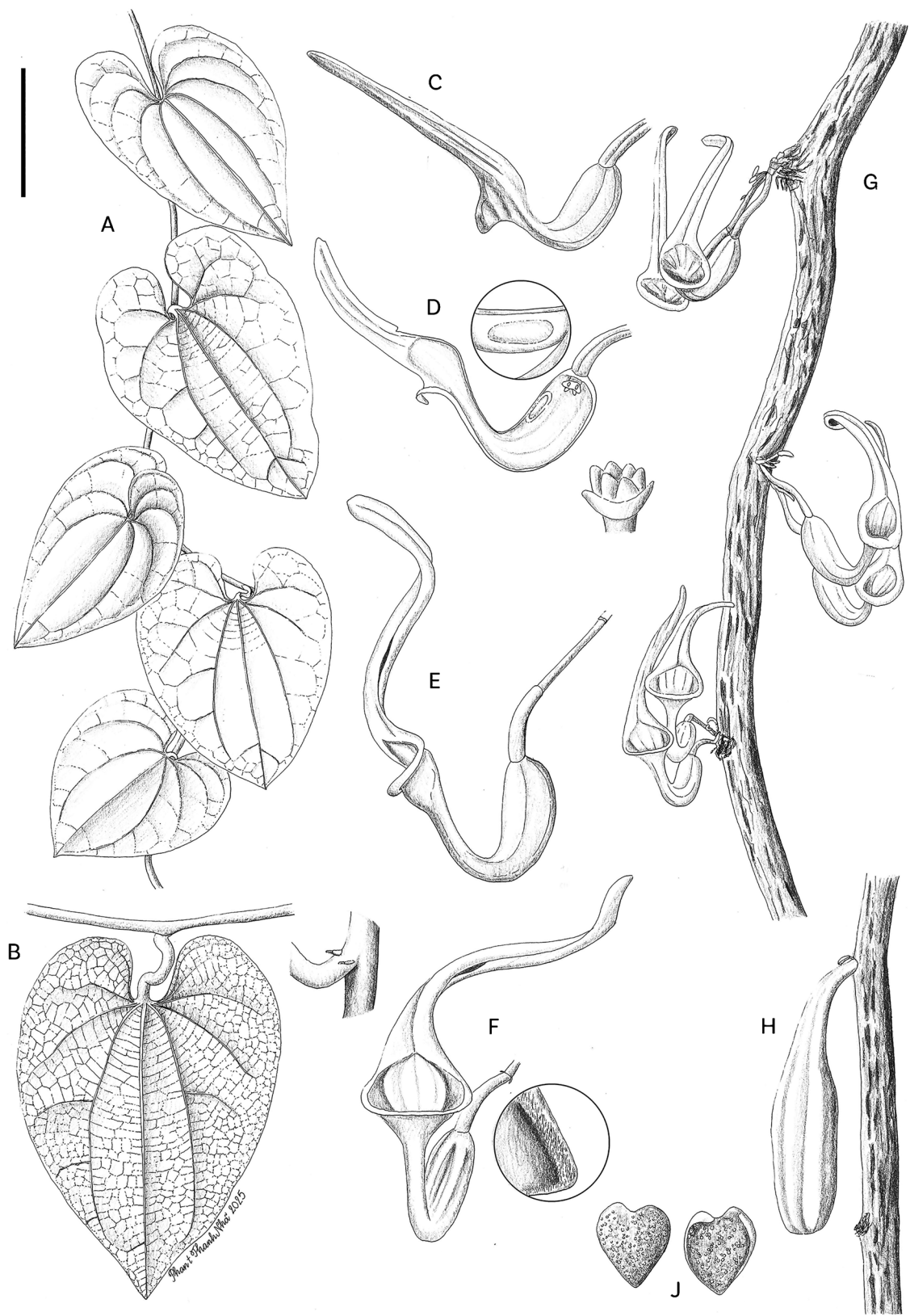


Fig. 4. *Aristolochia argilophila* sp. nov. **A** habit and leaves (adaxial); **B** leaf abaxial and node; **C** late preanthetic flower; **D** longitudinally dissected anthetic flower with magnified glandular body (inlet); **E** anthetic flower in lateral view; **F** anthetic flower in frontal view; **G** woody stem bearing flowers; **H** fruit; **J** seed abaxial (left) and adaxial (right). Scale bar: **A** 6 cm; **B** 5 cm; **C–F** 2.5 cm; **G** 6 cm; **H** 5 cm; **J** 1 cm. From the type specimen Frank, Andi, Jaafar, Abdullah & Pandai 2. DRAWN BY THANH NHÀ PHAN-THI.

114°28'36.2"E, 16 Sept. 2024 (fl., fr.), Frank, Andi, Jaafar, Abdullah & Pandai 5 (BRUN); Labi, Labi Forest Reserve, Bukit Telingan, 170 m, 04°22'N, 114°28'E, 7 June 1995 (fr.), Ahmad, Niga, Kalat, Hussain, Ibrahim & Clayton BRUN 16715 (L); Labi, Labi Hills, Bukit Telingan, Mixed Dipterocarp forest, 23 Oct. 1989 (st.), Wong BRUN 1592 (BRUN); Liang, Andulau FR, Compartment 19, 27 Sept. 1988 (st.), Wong s.n. (BRUN); Liang, Kg Sungai Liang, Andulau Forest Reserve, Roadside near Tangi Air Andulau, 85 m, 04°37'08.2"N, 114°30'16.9"E, 14 Sept. 2024 (fl.), Frank, Andi, Jaafar, Abdullah & Pandai 1 (BRUN); Liang, Kg Sungai Liang, Bukit Lumut, 53 m, 04°39'21.9"N, 114°28'25.2"E, 14 Sept. 2024 (fr.), Frank, Andi, Jaafar, Abdullah & Pandai 3 (BRUN); Liang, Liang, Andulau FR, Compartment 18, Jln Labi, behind water tank, roadside, 18 May 2015 (fl.), Kalat & Pandai BRUN 24397 (BRUN). Brunei-Muara: Serasa, Kampong Serasa, Bukit Tempayan Pisang, 100 m, N05°01', E115°02', 3 July 1995 (st.), Ismail, Kalat, Hussain, Ibrahim, Jangarun & Clayton BRUN 16850 (A, BRUN). Tutong: Tanjong Maya, Kpg. Bukit Kukub, 9 Jan. 1998 (fr.), Nyawa s.n. (BRUN); Tanjong Maya, Kpg. Bukit Udal, Bukit Kukub, Andulau FR, Compartment 57, 30 Jan. 2003 (fr.), Awok BRUN 19685 (BRUN).

CONSERVATION STATUS. *Aristolochia argilophila* is a narrowly distributed species endemic to northwestern Borneo (Brunei Darussalam, recorded from the Belait, Brunei-Muara, and Tutong districts). The species is currently known from 11 collections made between 1988 and 2024. Its Extent of Occurrence (EOO) is estimated at 1,013 km² and its Area of Occupancy (AOO) at 28 km² (after reduction analyses of 5% and 13%, respectively), both of which fall below the thresholds for listing as Endangered under Criterion B (IUCN 2012, 2024). The species is currently known from six locations, slightly above the threshold for Endangered but within the range for Vulnerable under Criterion B. Continuing decline in the extent and quality of its habitat is inferred, driven by ongoing and potential future threats such as urban expansion, fires, and land conversion. Although some subpopulations occur within forest reserves (Andulau FR and Labi FR), where habitat degradation is minimised, the species remains vulnerable across much of its range. Based

on its restricted distribution, limited number of locations, and inferred continuing decline in EOO, AOO, habitat quality, and number of subpopulations, *A. argilophila* qualifies as Vulnerable (VU) under criteria B1ab(i,ii,iii,iv)+2ab(i,ii,iii,iv).

PHENOLOGY. Flowers of *Aristolochia argilophila* have been observed from May to September. Fruits have been observed throughout the year.

ETYMOLOGY. The specific epithet *argilophila* is derived from the Greek *árgilos* [ἀργίλος] = clay, and *philos* [φίλος] = loving, referring to the species' marked edaphic preference for loamy, clay-rich soils, particularly the characteristic yellow clay found in parts of Brunei.

NOTES. In herbaria and literature, this species has been provisionally treated as *Aristolochia* cf. *foveolata* in Brunei Darussalam, as have most other cauliflorous *Aristolochia* lianas elsewhere in Borneo (Hou 1983a, b; Coode *et al.* 1996; Yao 2015). However, *A. foveolata* is a scrambling and twining herbaceous species with flowers in leaf axils of young shoots, described from the Philippine island of Luzon (Merrill 1918; Hou 1983b). Apart from *A. minutiflora* Ridl. ex Gamble, no records of other axillary-flowered subsection *Euaristolochia* entities have been reported south of this island in the Philippines. *Aristolochia minutiflora* can easily be distinguished from all other Bornean *Aristolochia* by the glaucous abaxial leaf surface and diminutive flowers (total size < 2 cm in length). A single, but cauliflorous subsection *Euaristolochia* record from Palawan is further discussed under notes of *A. transtillifera*. However, a thorough examination of diagnostic floral characters of cauliflorous lowland subsection *Euaristolochia* populations in Brunei Darussalam revealed notable differences compared to populations of morphologically similar entities in Borneo. The most obvious diagnostic character is the presence of 2 elongated glandular bodies inside the utricle of *A. argilophila*, whereas the morphologically closest subsection *Euaristolochia* entities, *A. transtillifera* and *A. papillifolia* from Borneo, as well as *A. foveolata* from the Philippines and Taiwan, possess 6 glandular bodies. Only a morphologically more distant entity, *A. naviculilimba* Ding Hou, has been described with 2 glandular bodies from Sarawak and Kalimantan but differs strongly by the shape of the perianth, especially limb and utricle, as well as the absence of trichomes on the limb (Hou 1983a). The elongated obpyriform utricle of *A. argilophila*, as well as the inclination angle of late preanthetic flowers, and length of the limb, sets it further apart from all morphologically closer congeners on Borneo, especially *A. transtillifera* and *A. papillifolia* (Table 1). It is worth mentioning that although the cauliflorous *Aristolochia* populations on Borneo have been mostly referred to as one variable entity *A. foveolata*, this variation appears to be only of vegetative nature, while the



Map 1. Distribution of *Aristolochia papillifolia*, *A. transtillifera* and *A. argilophila*. Note that localities with vegetatively 'typical' *A. transtillifera* are highlighted in white triangles.

floral characters are consistently different with no clinal variation observed. *Aristolochia argilophila* is grown occasionally by butterfly breeders and zoological institutions as host plant for rearing *Troides* Hübner, 1819 and *Ornithoptera* Boisduval, 1832 species, mostly under the previous name of *A. cf. foveolata* (Jalil *et al.* 2008; Sutton *et al.* 2021). Although *A. argilophila* is currently only known from low elevations across Brunei Darussalam, it appears probable that it occurs in the adjacent lowlands of Sarawak.

Aristolochia transtillifera Ding Hou

Woody liana. *Stems* terete, 3.5 – 6 mm in diameter, occasionally slightly striated, glabrous when young, with corky bark when mature, internodes 5 – 15 cm long, pseudostipules absent. Broken stems emit a scent similar to orange. *Leaves* marcescent, leaving petiole remnants after decomposing; petiole 3 – 7 cm long. Lamina subcoriaceous, cordiform-ovate, ovate-oblong to oblong-elliptic, measuring 11 – 24 × 4 – 11 cm, basally cordate, obtuse or subtruncate with wide sinus 0.1 – 1 cm deep to absent, apically acuminate. Adaxial surface glabrous, abaxial surface papillate. *Inflorescences* cymose, with 1 – 10 flowers, cauliflorous. Bracts ovate, glabrous. *Flowers* protogynous, peduncle

plus ovary 3 – 4.5 cm long (at anthesis), glabrous, perigone geniculate. Outer surface glabrous, brownish-beige to purplish-brown. *Utricle* rounded to obovoid, gibbous, 0.6 – 0.8 × 0.5 – 0.7 cm, inner surface purple-brown, densely covered by short white trichomes with tomentose appearance. Glandular bodies 6, rounded. Syrinx absent. *Tube* cylindric, 0.8 – 1.5 cm long, inner surface beige to yellow, densely covered by white trichomes. Fauces round, beige transitioning to dark purple with white trichomes. *Limb* unilabiate, oblong-lanceolate, 2.5 – 4 × 0.8 – 1.2 cm, inclination angle 80 – 125°, glabrous, brown to dark purple, white trichomes covering more than half of the limb length, apex mucronate. *Gynostemium* coroniform, 0.4 – 0.5 × 0.3 – 0.5 cm. Stigmatic lobes 6, beige in colour. Anthers 6, short-oblong, c. 0.1 cm. *Fruit* capsules cylindric, 3 – 4 × 1 – 1.8 cm, apex rounded, glabrous, with basal, septicidal dehiscence. *Seeds* triangular to obovate, 0.5 – 0.6 × 0.3 – 0.5 cm, non-winged, dark brown, abaxial surface papillate, adaxial side with sticky elaiosome present.

DISTRIBUTION. *Aristolochia transtillifera* is distributed in the Philippines (Palawan), northern Borneo, specifically in western Sabah (Malaysian Borneo) and Temburong district (Brunei Darussalam). Its range likely extends into the narrow intervening area of Sarawak that lies between these regions.

HABITAT. *Aristolochia transtillifera* inhabits primary and secondary lowland to lower montane forests, from 30 – 1500 m elevation, often along riverbanks, forest edges, and disturbed sites. It typically grows in shaded to semi-shaded conditions, climbing over shrubs and into the canopy of trees, and is frequently associated with moist, well-drained soils.

SPECIMENS EXAMINED. THE PHILIPPINES. Palawan: Palawan central, Irawan, Puerto Princesa, 8 Dec. 1965 (fl.), Jumalon s.n. (L). **MALAYSIA.** Sabah: Beaufort, Beaufort Hill, Phaenological plot, 30 m, 5°20'85"N, 115°45'00"E, 7 Dec. 1961 (fr.), Rivera SAN 19008 (holotype SAN, isotypes K, L); Keningau, Crocker Range NP, Crocker Range FR, Mile 9 Keningau-Kimanis road, 5°34'N, 116°39'E, 1 Oct. 1981 (st.), Aban, Meijer & Sundaling SAN 94104 (SAN); Keningau, Kimanis-Keningau Road, Crocker Range, 9 Nov. 1994 (fr.), Repin & Benedict SP 6992 (SNP); Keningau, Ulu Sg. Matud logged area, 5°32'N, 116°16'E, 27 June 1987 (fr.), Fidilis & Sumbing SAN 119582 (SAN); Kota Belud, Penataran basin, 5000 ft, 24 July 1933 (st.), Clemens & Clemens 34096 (A); Papar, Crocker Range, Kimanis to Keningau, 05°30'N, 116°00'E, 2 Sept. 2002 (fr.), Takano & Johnny 108 (BORH); Penampang, Crocker Range Park, Sub-Station Inobong, 31 Oct. 2007 (fl., fr.), Yabainus, Geofarry, Hadimin, Betricia & Kaidin KNP 14555 (SNP); Penampang, Sinsuron Road, Central Crocker Range, 300 m, 18 Feb. 2013 (fl.), Lamb & Philipps SAN 2431/2013 (SAN); Ranau, 5000 ft, 1931 – 1932 (fr.),

Clemens & Clemens 26639 & 28732 (A, K, L); Ranau, Gurulau spur, Jungle ridge, 5000 – 7000 ft, 5 Dec. 1933 (st.), *Clemens & Clemens* 50728 (A); Ranau, Kampung Bundu Tuhan, Notoki, 10 Sept. 1994 (st.), *Soibeh* 832 (SNP); Ranau, Kampung Menggis, 5 Oct. 1996 (fr.), *Rumutom* 450 (SNP); Ranau, Kinabalu Mountain Lodge, 1540 m, 06°00'36.63"N, 116°32'01.8"E, 15 Aug. 2018 (st.), *Burger & van der Linden* SNP 40974 (SNP); Ranau, Kinabalu Mountain Lodge, 1524 m, 06°23'23.37"N, 116°31'56.53"E, 15 Aug. 2018 (st.), *Burger & van der Linden* SNP 40975 (SNP); Ranau, Mt Kinabalu; Eastern Shoulder, 3000 ft, 06°05'N, 116°36 – 40'E, 21 June 1961 (st.), *Chew, Corner & Stainton* 129 (L); Sipitang, Meligan, Road to Meligan, 5 miles from Kpg. Mendolong, 4°40'30"N, 115°42'15"E, 6 Sept. 1983 (fr.), *Lee & Sundaling* SAN 69218 (SAN); Tambunan, Crocker Range, km 58 on Kota Kinabalu – Tambunan road, 1450 m, 05°47'N, 116°20'E, 18 Dec. 1983 (fr.), *Beaman, Beaman & Mellichamp* 7914 (A, L); Tambunan, Trus Madi FR, 1465 m, 5°34'27"N, 116°29'04"E, 5 Aug. 2009 (st.), *Pius, Joel & Postar* SAN 146449 (K, L, SAN). Tenom, Melalap, Kg. Sumbiling route to Tarang Teli, 740 m, 27 Jan. 2004 (st.), *Sumbin* SP 18248 (SNP). **BRUNEI DARUSSALAM.** Temburong; Batu Apoi, Bukit Gelagas, vicinity of camp site and landing place, 350 m, 4°20'24"N, 115°09'00"E, 29 Oct. 1991 (fr.), *Simpson & Marsh* 2507 (K, L).

PHENOLOGY. Flowers have been recorded between August to January, and fruits have been observed from June to February. It is likely that this species fruits throughout the year. Flowering appears to be particularly induced in drier or exposed spots, for example when the plants are disturbed (roadside, logging path, fallen tree).

ETYMOLOGY. The specific epithet was given for the 'many transverse veins connecting the palmate nerves', a character further discussed under notes.

NOTES. For a long time, *Aristolochia transtillifera* was reported only from the type locality in Sabah, Beaufort district on "Beaufort Hill" (today possibly Bukit Bendera) in primary forest at approximately 30 m altitude (Hou 1983a). Specimens with the originally described obovate to almost elliptic lamina have since only been recorded five times to date across the Crocker Range as far south as to Brunei on the border with Sarawak. Notably, the sheet of the type specimen deposited at SAN exhibits the elliptic leaves as well as leaves with a shallow sinus, hinting at variation within the *sensu stricto* described individual as well. We here amend its original description by including the floral characteristics first recorded in a vegetatively 'typical' specimen collected in 2009 at Inobong Substation, Crocker Range Park, now deposited at SNP (*J. Yabainus et al.* KNP 14555). The perpendicular veins, described as diagnostic for this taxon, have been reported in *A. papillifolia* and *A. argilophila* as well since the original description. To our current

knowledge and field observations, the flowers of the vegetatively 'typical' *A. transtillifera* are not different to flowers from populations of Mt Trusmadi, Nuluhon Trusmadi Forest Reserve in Tambunan, to other specimens with more cordiform leaves in the Crocker Range, and to specimens reported from around Mt Kinabalu. Furthermore, we observe in vouchers and our own observations that the leaf shape even along the same stem can drastically transit from cordiform to oblong-elliptic within less than 6 – 7 leaves (personal observations, and vouchers, e.g.: *Clemens et al.* 26639 – 28732 [L!]). We were not successful relocating *A. transtillifera* at the type locality twice (2023, 2024), and in widespread evidence of extreme vegetative plasticity observed in mainly sympatric records we interpret the type specimen and the four vegetatively 'typical' records merely as extremes of vegetative variation. This hypothesis is further confirmed by geometric morphometry of the leaves, which shows that the variation of leaf shape between *sensu stricto* *A. transtillifera* and *A. papillifolia* is actually much more plastic than inferred from the respective type specimens. Nevertheless, more records of vegetatively 'typical' specimens are urgently required to make a more thorough assessment regarding the vegetative natural variation of this entity. We also list a record of a cauliflorous subsection *Euaristolochia* entity from Palawan, the Philippines, under this taxon, given that it does not match the original description of *A. foveolata* as an axillary-flowered plant (Merrill 1918; Hou 1983b). We have not seen living specimens of the populations from Palawan, yet by examination of preserved flowers and photographic records we find more characters aligning with *A. transtillifera* than *A. papillifolia*.

ADDITIONAL SPECIMENS EXAMINED OF *Aristolochia papillifolia*. **MALAYSIA.** Sabah: Beluran, Labuk Sugut, Lung Manis, 5°41'N, 117°39'E, 11 May 1962 (fl., fr.), *Mikil* SAN 34658 (holotype SAN, isotypes K, L); Keningau, Pensiangan Kayu Forest Reserve, 4°49'N, 116°18'E, 25 Oct. 1985 (fr.), *Fidilis & Sumbing* SAN 113001 (SAN); Kinabatangan, Imbak Valley, Gunung Kuli Trail, 460 m, 5°01'20"N, 117°03'05"E, 28 Nov. 2010 (fr.), *Yao & Nor Ezzawanis* FRI 74259 (KEP, L, SAN); Kinabatangan, Ulu Sungai Pinangah, 4°44'45"N, 116°37'00"E, 29 Aug. 1984 (fl.), *Madani & Sundaling* SAN 60443 (SAN); Lahad Datu, Danum Valley and environs, Bole river, 23 June 1989 (st.), *Ridsdale* 2138 (L, SAN); Lahad Datu, Kawag Danum Rain Forest Lodge, 26 May 2016 (fl.), *Repin, Geofarry, Kinahim, Kalapin & Yabainus* SNP 40456 (SNP); Nabawan, Pandewan, Sungai Mesopo, 4°56'00"N, 116°28'30"E, 26 Feb. 1986 (st.), *Fidilis* SAN 114055 (SAN); Sipitang, Long Pasia, Expdisi Ulu Padas, Base Camp, 3400 ft, 26 Jan. 2003 (fr.), *Sumbin* SP 18059 (SNP); Tawau, Kelumpang Balong, 76 m, 4°33'N, 118°10'E, 7 June 1961 (fr.), *Bakar* SAN 17334 (L, SAN); Tongod, Kampung Saguan, Pinangah, 180

m, 18 July 1981 (fr.), *Sundaling* SAN 93778 (L, SAN, SAR). Sarawak: Samarahan, Gunung Buri, 75th mile, 1st/2nd Division boundary, 600 m, 13 Sept. 1975 (fr.), *Chai* SAR 36697 (K, L, SAN). **BRUNEI DARUSSALAM.** Temburong: Amo, Kuala Belalong National Park, along Sg. Temburong, 6 Sept. 1993 (fr.), *Kalat & Ibrahim* BRUN 15157 (BRUN); Bangar, Labu, Bukit Patoi, 225 m, 4°44'59.7"N, 115°10'31.2"E, 15 Sept. 2024 (st.), *Frank, Andi, Jaafar & Pandai* 4 (BRUN).

Discussion

Borneo, a megadiverse island with a complex ecosystem, remains understudied in terms of *Aristolochia* taxonomy. While iconic butterfly species such as Raja Brooke's Birdwing, *Trogonoptera brookiana* (Wallace 1855), and Kinabalu Birdwing, *Troides andromache* (Staudinger 1892) are comparably well-studied, *Aristolochia* as their host plants remain poorly understood (Jalil *et al.* 2008; Sutton *et al.* 2021). Since Hou's (1983a, b) revisions, no comprehensive taxonomic updates have been conducted for this genus in Borneo, and extensive collections in Sarawak and Kalimantan are lacking. This study represents a first milestone in revising *Aristolochia* species of Borneo and the wider indopacific area, revealing inconsistencies in existing species definitions. Our data suggest substantial changes are required to the taxonomy of *Aristolochia*, particularly regarding the species currently placed under the broadly defined *papillifolia* group and previously under *A. foveolata*. The lack of thoroughly documented reproductive structures, especially flower, fruit and seed morphology, continues to obscure the genus's diversity in this region. Several subsequent studies in preparation are intended to address the elusive diversity of this genus on Borneo and surrounding islands.

The papillate abaxial leaf surface was described as the diagnostic character of *Aristolochia papillifolia* (Hou 1983a, b). In contrast to the initial diagnosis, we cannot confirm that this character is unique to *A. papillifolia*. We have observed the same characters in most cauliflorous *Aristolochia* specimens in Borneo, especially in young leaves, which suggests that this feature might be worn off as the leaves become older and gain their coriaceous appearance. Our observations further indicate that flowers of all cauliflorous vines from Borneo classified under *A. foveolata* differ significantly from *sensu stricto* Philippine and Taiwanese *A. foveolata* (type locality of *A. foveolata*: Catanduanes, Luzon) but align more closely with the Bornean taxa *A. papillifolia* and *A. transtillifera*. Thus, we propose to exclude *A. foveolata* from the Flora of Borneo. It appears that the *papillifolia* group as well as its close congeners encompass multiple distinct taxa overlooked due to the lack of thoroughly documented diagnostic reproductive characters. Widespread tropical and subtropical *Aristolochia* species and

entire taxonomic groupings frequently are extremely plastic in terms of vegetative appearance (Blanco 2002; De Groot *et al.* 2006; Saldivia & Faúndez 2015; Freitas *et al.* 2020).

Seeds of congeners of the *papillifolia* group are dispersed via a comparably short range by insect attraction (e.g. wasps, ants) to the fatty elaiosome attached to the adaxial part of the seed (Sven Landrein, personal observation). In contrast, seeds of the Bornean *Aristolochia acuminata* Lam. and *A. jackii* Steud. are wind-dispersed, and these two species are frequently found in coastal areas and colonising logged land. These two species belong to subsection *Podanthemum* are widespread between SE Asia to Polynesia and also exhibit extreme leaf diversity (Hou 1983b; De Groot *et al.* 2006; Yao 2015). Despite this, relatively consistent floral morphology was observed both in the field and in herbarium specimens across these species' distribution ranges (unpublished data). For the case of Borneo, it can be hypothesised that subsection *Podanthemum* species with wind-dispersed seeds show larger distribution areas while subsection *Euaristolochia* species, like the affinities of the *papillifolia* group might be more restricted in their distributional patterns (e.g. due to ecological factors such as less widespread seed dispersal, edaphic, climatic or altitudinal factors). This is mirrored here by the discovery and description of a new species, *A. argilophila* with a comparably small distribution area, and preference for loamy soil in coastal Brunei Darussalam.

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Declarations

Conflict of interest The authors declare that they are unaware of any conflicts of interest.

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