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Journal of Plant Taxonomy and Geography (*Webbia*) is a peer-reviewed journal on Plant Taxonomy, Nomenclature, Phylogeny, Phytogeography and Paleobotany. Most of the contributions deal with the Vascular Plants, but sometime contributions on Briophytes, Lichenes, Fungi and Algae are encouraged.

The journal aims to allow research in botanical topics such as taxonomy, systematics, nomenclature, molecular phylogeny, conservation, biogeography, and history of botany, and botanical collections.

It was founded in **1905** in Florence by **Ugolino Martelli** (1860-1934), a botanist well known for his studies of and contributions to the systematics of the tropical genus *Pandanus* and on the Flora of Sardinia.

In the 19th century Florence represented one of the most important European centres in Plant Taxonomy and Phytogeography with several notable Italian botanists worth mentioning such as Filippo Parlatore, Teodoro Caruel, Eugenio Baroni, Stefano Sommier, Odoardo Beccari and Ugolino Martelli himself. In 1842 **Filippo Parlatore** (1817-1877) founded in Florence the *Herbarium Centrale Italicum (FI)*, which soon became one of the most important herbaria in the world. Most of the specimens described and/or cited in *Webbia* are still kept in it.

In 1905, and as a consequence of this multitude of activities in Plant Systematics and Phytogeography, Ugolino Martelli established the journal *Webbia-Raccolta di Scritti Botanici*, firstly published annually in a single issue, and later twice a year. Webbia also began to be a place of publication of contributions from Tropical Botany, especially after the Royal Colonial Herbarium founded in 1904 in Rome was moved to Florence in 1914, currently named Tropical Herbarium Study Center (Centro Studi Erbario Tropicale - Herbarium FT) belonging to the Department of Biology of the University of Florence.

Webbia had been created in honor of **Philip Barker Webb** (1793-1845), a close friend of Filippo Parlatore, who before passing away entrusted his personal herbarium and a library rich of old botanical books and publications to the then Botanical Museum in Florence.

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Comments

The impact of Covid-19 crisis on Plant Taxonomy: will we be able to approach to plant taxonomy as in the past?

There is no doubt that the current global crisis due to Covid-19 is changing our lives and our future habits, but we must hope that the situation will slowly get better.

Nonetheless, we should all reflect more on our future, including our personal life and professional work, considering that the effects of the current pandemic will also significantly affect the research activity of plant taxonomists in the coming times.

One of the aspects that will be most affected will be field research, starting from its logistic organization up to authorization by the competent territorial authorities, especially in tropical areas. Hopefully, expeditions will not be impossible in the future, but we can surely expect additional complications that will slow down experimental research in the field and possible also simple travelling, collecting activities and field courses.

We are currently witnessing a complete stalemate in field research and may expect slow-down and restrictions at least for some time to come due to limitations in travelling, especially overseas travelling. Already, field research is per se limited in time by seasonality and the best time to collect the study material, be it plant or animal.

Visits to herbaria will also be affected, due to the necessary procedures that are being adopted to guarantee sanitary security and to avoid infection through the handling of herbarium collections. The current reasonably large availability of digitized information has become really crucial in this situation. Nonetheless, we know that interpretation of digital images cannot always substitute direct examination of specimens and that the majority of the World's herbarium collections are not yet digitalized. We also know that visiting a herbarium does not only consist of studying its collections, including associated libraries. It represents an occasion to meet and exchange information with colleagues: an opportunity of professional empathy.

Another consequence may be seen in a foreseeable further reduction of the funding of plant taxonomic research. Funding of plant taxonomy is already inadequate, and there is a real danger that even launched projects cannot be completed on time and may therefore run out of funds. We must not forget that these difficulties encountered by senior scientists, will also influence the thesis activities of under- and post-graduate students, who risks seeing their study schedule compromised, with consequences for family budgets or even their future careers.

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Recurring conferences, symposia, celebrations will not take place now, and probably they will not do so for a long time. It is true that many scholars –including some plant taxonomists – who regard travelling for many hours by plane as a cause of severe ecological damage, would rather opt for events to be held remotely whenever possible. However, I cannot feel happy to miss at least some personal contacts with colleagues if I have to avoid all travels for scientific meetings!

Let's be realistic! At present, we can only wait with wise patience for the end of this nightmare that is gripping the whole world and also our community of plant taxonomists. In the meantime, we must concentrate on guaranteeing the transmission of our discipline by remote teaching, and devote time to completing and publishing, wherever possible, our current investigations. We must try to maintain and amplify our contacts and collaborations with a perspective on the future. In particular, as teachers in Plant Taxonomy, we must not lose contact with your students and especially with those who demonstrate a genuine and concrete interest in our discipline.

Riccardo M. Baldini

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Nepenthes latiffiana and *N. domei* (Nepenthaceae), two new species of pitcher plants from Terengganu, Peninsular Malaysia

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Abstract. Two new species of *Nepenthes* from Terengganu, Peninsular Malaysia, *N. latiffiana* M. N. Faizal, A. Amin & N. Dome and *N. domei* M. N. Faizal, A. Amin & A. Latiff, are described and illustrated.

Keywords: pitcher plants, carnivorous plants, *Nepenthes, Nepenthes domei, Nepenthes latiffiana,* Terengganu, Peninsular Malaysia.

INTRODUCTION

In Peninsular Malaysia, a total of eleven species of pitcher plants *(Nepenthes)* or locally known as “periuk kera” have been recorded (Jebb and Cheek 1997; Cheek and Jebb 2001; Clarke 2001; McPherson 2009). The first taxonomic account of the genus in Peninsular Malaysia was given by Ridley (1924) who recorded a total of ten species, namely *N. ampullaria* Jack., *N. albomarginata* Lobb., *N. gracillima* Ridl., *N. alba* Ridl., *N. ramispina* Ridl., *N. sanguinea* Lindl., *N. macfarlanei* Hemsl., *N. gracilis* Korth., *N. rafflesiana* Jack and *N. phyllamphora* Willd. (= *N. mirabilis* (Lour.) Druce). After Ridley’s treatment, there have been some further researches on the genus by Holttum (1940), Kiew (1990), Turner (1995), Clarke (2002), Adam et al. (2005) Latiff et al. (2011), Clarke and Lee (2012) and Latiff and Norsiah (2016) regarding the diversity, distribution, and ecological study of *Nepenthes* species and natural hybrids. Another taxonomic study of the Peninsular Malaysian taxa was carried out by Rohana in 1988 that covers basic anatomical features and systematic study of the species and hybrids. Turner (1995) listed ten species, which instead included two natural hybrids, namely *N.* × *hookeriana* and *N.* × *trichocarpa*, with *N. alba* and *N. ramispina* being excluded. Clarke (1999) added *N. benstonei*, a species then known from Bukit Bakar, Kelantan, to the list and the latest was Adam and Hamid (2007) who described *N. sharifah-hafsahii* which happens to be a natural hybrid between *N. gracilis* and *N. mirabilis* rather than a true species (McPherson 2009).

The most comprehensive and well accepted taxonomic enumeration works of the genus were given by Jebb and Cheek (1997), Cheek and Jebb (2001) and Clarke (2001) who recognised eleven species. In the course of continuous field trips to the state of Terengganu, the authors had encountered several populations of pitcher plants in Setiu whose features did not match the currently described taxa of Peninsular Malaysia. From this finding, we further analysed the morphological, anatomical and micromorphological characteristics and have discovered two distinct new species (as described in this article). The descriptions of *N. domei* and *N. latiffiana* herein can be considered as a comprehensive work in the taxa identification as the sheet contains the sterile/fertile parts and pitchers, anatomical and micromorphological evidences, and enumeration of prominent plant characteristics. We also conducted a comparative molecular study on *N. domei* using internal transcribed spacer (ITS) DNA region to further differentiate it from a closely related species.

MATERIALS AND METHODS

Analyses of morphological characteristics on new *Nepenthes* specimens were based on living plants observed *in situ* and also from herbarium type specimens (MDI12424 and MDI12423) deposited at MARDI Herbarium (MyGenebank™ Complex MARDI Serdang).

For leaf anatomy analysis, collected and described *Nepenthes* leaves were fixed in AA solution (1 Acetic acid : 3 Alcohol). Investigated leaf parts including midrib, lamina and margin were sectioned in a range of thickness from 15-30 μm using sliding microtome. The leaves then were cleared using bleaching agent, washed in various alcohol series and stained in Safranin and Alcian blue for 5 minutes each before proceeded for dehydration stage through an ascending alcohol series (50-100%). During the final dehydration stage, the leaf specimens were differentiated in 70% alcohol with a drop of hydrochloric acid (HCL) before mounted in Euparal. Specimen slides were kept in the oven for two weeks at about 60-70°C. Photographs of the investigated sections were taken using Olympus SZH40 microscope and the images were processed using CellSens Image Analysis software.

For micromorphology study, *Nepenthes* epidermis preparative fragments about 3 mm long were excised from the middle portion of approximately three mature leaves of each species. Cuticle parts were prepared by soaking leaf blade fragments in 5-10% aqueous chromium trioxide until all organic material except the cuticle was dissolved. Targeted leaf cuticles were mounted on aluminium stubs with double-sided adhesive tape and proceeded for air drying. The stubs were then sputter-coated with pure gold to a maximum thickness of 15 nm and examined with LEO (Model 1450 SEM) - Field-Emission Scanning Electron Microscope (FESEM). The remaining cuticles were soaked in 5% ammonia and mounted on microscope slides in Canada balsam.

Results of the adaxial and abaxial epidermal layers under scanning electron microscope (SEM) and leaf anatomical study of *N. domei, N. latiffiana*, *N. benstonei* and *N. sanguinea* are shown in Figure 5 to 12 and summarised in Table 2 and 3. These results are combined with transverse section of the leaf lamina and margin showing epidermal cells, mucilaginous idioblast, glandular and simple trichomes, solitary crystals observation on the parenchyma and along a vein, and significant venation characters. The systematic significant of leaf anatomy and micromorphology evidences differentiating these investigated *Nepenthes* species are presented in Table 2 and 3.

Finally, for molecular study, all genomic DNA purifications were done according to DNeasy Plant Mini Kit (Qiagen) manufacturer's protocol and matured leaves (100 mg per sample) from *N. domei* sp. nov. (Terengganu), *N. benstonei* (Bukit Bakar, Kelantan) and *N. sanguinea* (Fraser's Hill, Pahang) were used. The internal transcribed spacer (ITS) partial gene (~610bp) was PCR-amplified from *Nepenthes* DNA using universal ITS1-2 primers (ITS_F: 5'-AGGAGAAGTCGTAACAAGGTT; ITS_R: 5' GATGCAACCTTGGCCTT) and Q5 High-Fidelity DNA polymerase (New England Biolabs, UK). The parameters for thermocycler were set as follows: initial denaturation at 98°C for 30 s, denaturation at 98°C for 10 s, annealing at 61°C for 15 s, extension at 72°C for 20 s, and final extension at 72°C for 2 min. The amplicons were sent for Sanger sequencing and the sequencing data was trimmed and aligned using BioEdit Sequence Alignment Editor. Phylogenetic inference of nine peninsular *Nepenthes* species (including *N. domei* sp. nov.) was reconstructed in Molecular Evolutionary Genetics Analysis software (MEGA5) using Neighbor-Joining (NJ) method (1000 bootstraps) based on the ITS partial sequences isolated in this study as well as sequences obtained from the NCBI database (Bunawan et al. 2017; Alamsyah and Ito 2013; Renner and Specht 2011).

TAXONOMIC TREATMENT

Nepenthes latiffiana M. N. Faizal, A. Amin & N. Dome, **sp. nov.** (Figures 1 & 2)

Type: Malaysia, Peninsular Malaysia, Terengganu, Setiu, 30 April 2019, MNFG751 (MDI!), MDI12424, *Mohd. Norfaizal, Amin Asyraf, Dome Nikong, Muhamad Ikhwan, Edward Entalai & Anuar Rasyidi*, [holotypus, MDI]

Diagnosis

Nepenthes latiffiana differs from *N. sanguinea* in peristome morphology which is considerably developed, loosely cylindrical, with expanded outer margin part towards both sides of the mouth forming flap-like structure which is especially prominent in upper pitcher (vs. simple, expanded, outer margin usually markedly sinuate where the peristome is widest); climbing stem with simple hairs, cross section cylindrical (vs. glabrous, sharply angular) and lid margin slight wavy to wavy that retains its morphology in dried and wet preserved specimens (vs. flat).

Description

Terrestrial climber to 0.5-1.5 m tall. *Climbing stems* cylindrical to rounded, particularly towards the leaf nodes, 0.8-1.2 cm in diameter. *Internodes* 2.2-3.5 cm long. *Leaves* coriaceous, sessile to less amplexicaul, linear-lanceolate, apex obtuse to emarginated, 15-20 cm long, 5-6 cm wide; base clasping stem for about ½ of its circumference; longitudinal veins 1-3 on each side of the midrib, pennate nerves conspicuous; tendril with slender formation in the middle, 10-14 cm long, with minute hairs. *Lower pitchers* up to 18-26.5 cm long, 4.9-8 cm wide, fleshy coriaceous texture, arising abruptly from the tendril; broad cylindrical at the lower part of the pitcher, ½ upper of the pitcher slightly swollen with hip formation, 9 cm length, up to 7 cm above of the hip till nearly closer to the mouth; cylindrical above, with slight widening towards the mouth, surface of the hip smooth; two fringed wings up to 0.9-1.0 cm wide, runs along the pitcher and widest at the mouth, with multicellular hair elements up to 0.3-0.6 cm long; spur with branched form, reaching 1.0 cm long; mouth rounded; peristome loosely cylindrical but widening or expanded towards lateral sides of the pitcher mouth (ca. 1.5 cm wide each side), outer surface smooth, reaching 1.1 cm wide (in front of the mouth), ribs (at the part of the peristome) reaching 1.6 cm wide; lid rounded, up to 6.5 cm long and 6 cm wide, base retuse, without appendages or trichomes on the lower surface of the lid, ~105-126 dotted nectar glands superfluous and dense at the center and base of the lid. *Upper pitchers* up to 20-23.5 cm long, 5-7.5 cm wide, coriaceous texture, arising slight abruptly from the tendril; broad cylindrical at the ¼ lower part of the pitcher, ¾ upper of the pitcher cylindrical and slight narrowing towards the mouth; with minute wings; mouth ovoid to sub ovoid, peristome cylindrical but with expanded lateral sides (1.3-1.4 cm wide each side) and flattened towards the front of the mouth part, outer surface smooth, reaching 9mm wide, ribs reaching 1.3 mm wide; lid rounded, up to 4.8-5.2 cm long and 5.5 cm wide, base cordate, without appendages or trichomes on the lower surface of the lid. *Male inflorescence* a raceme, peduncle up to 16 cm, rachis up to 40 cm, partial peduncles single-flowered, bracts absent, pedicel 10-13 mm long, tepal ovate, up to 2-5 mm, staminal column 2.5-6 mm long, anther head 2-3.75 mm. *Colour of the living plants:* Lower pitcher combination of green-yellowish-brown hues with several red blotches formation on the 1/3 of the upper part of the pitcher body. Upper pitcher light green with fade specks. Pitcher interior green-yellowish to reddish. Leaves green. Stem green to dark green. *Colour of the dried specimen* light brown – pale brown (lamina, stem and pitcher).

Etymology

Named in honour of Emeritus Professor Dato' Dr. A. Latiff Mohamad, a prominent figure in Malaysian Botany Field from Universiti Kebangsaan Malaysia, Bangi Campus, Malaysia.

Distribution and habitat

Nepenthes latiffiana is currently known only from the restricted area at the type locality in Setiu, Terengganu.

Ecology

Nepenthes latiffiana occurs as terrestrial climbers on hilly terrains with slight shaded, upper hill forest habitats, at an altitude of c. 1000-1100 m.

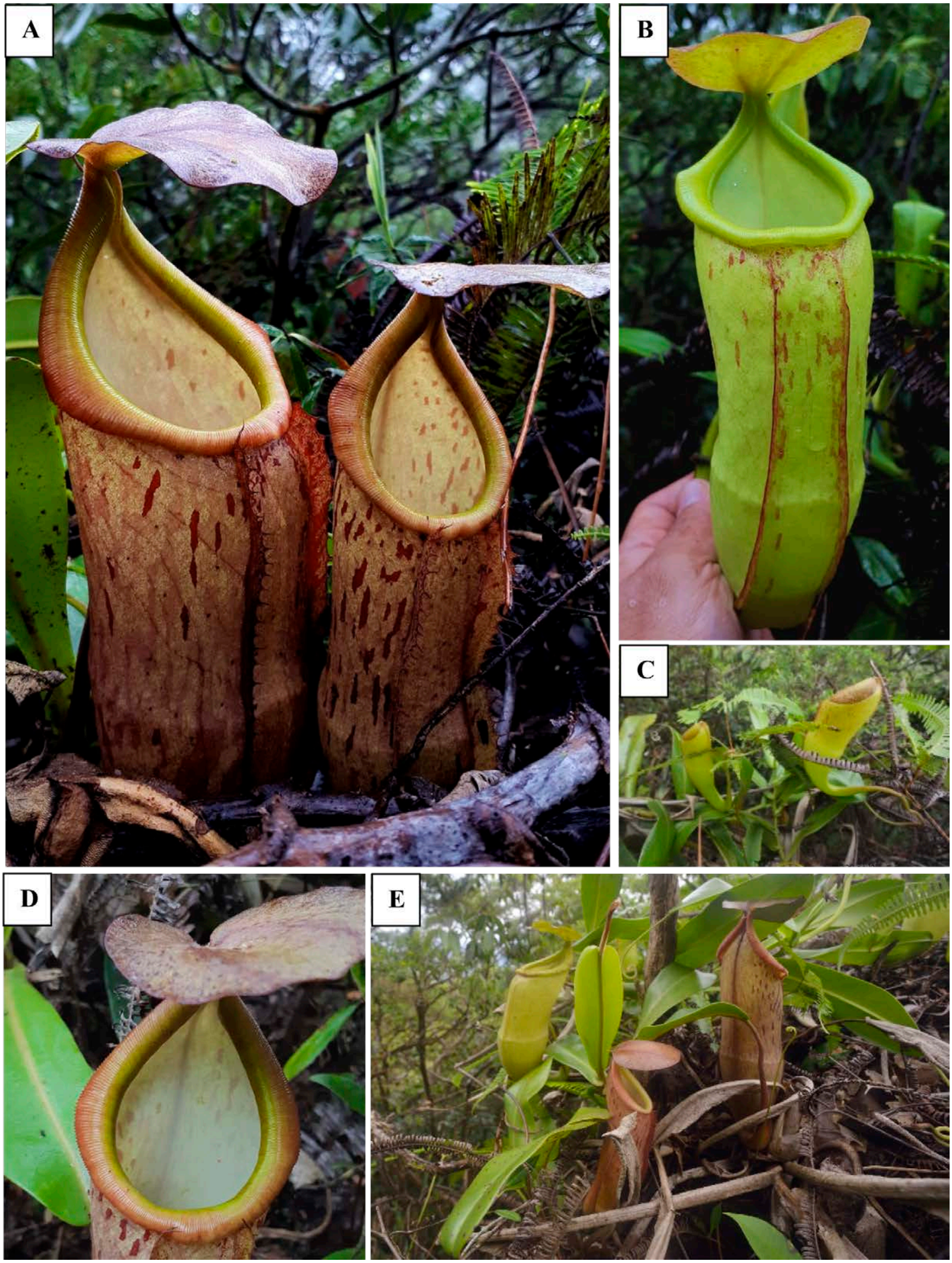

Figure 1. *Nepenthes latiffiana*, in situ: **(A)** Lower pitchers. **(B)** Upper pitcher. **(C)** Immature upper pitchers. **(D)** Lid, peristome and waxy inner surface of lower pitcher. **(E)** Habit showing the lower and upper pitchers. Photographs by Mohd Norfaizal Ghazalli and Amin Asyraf Tamizi.

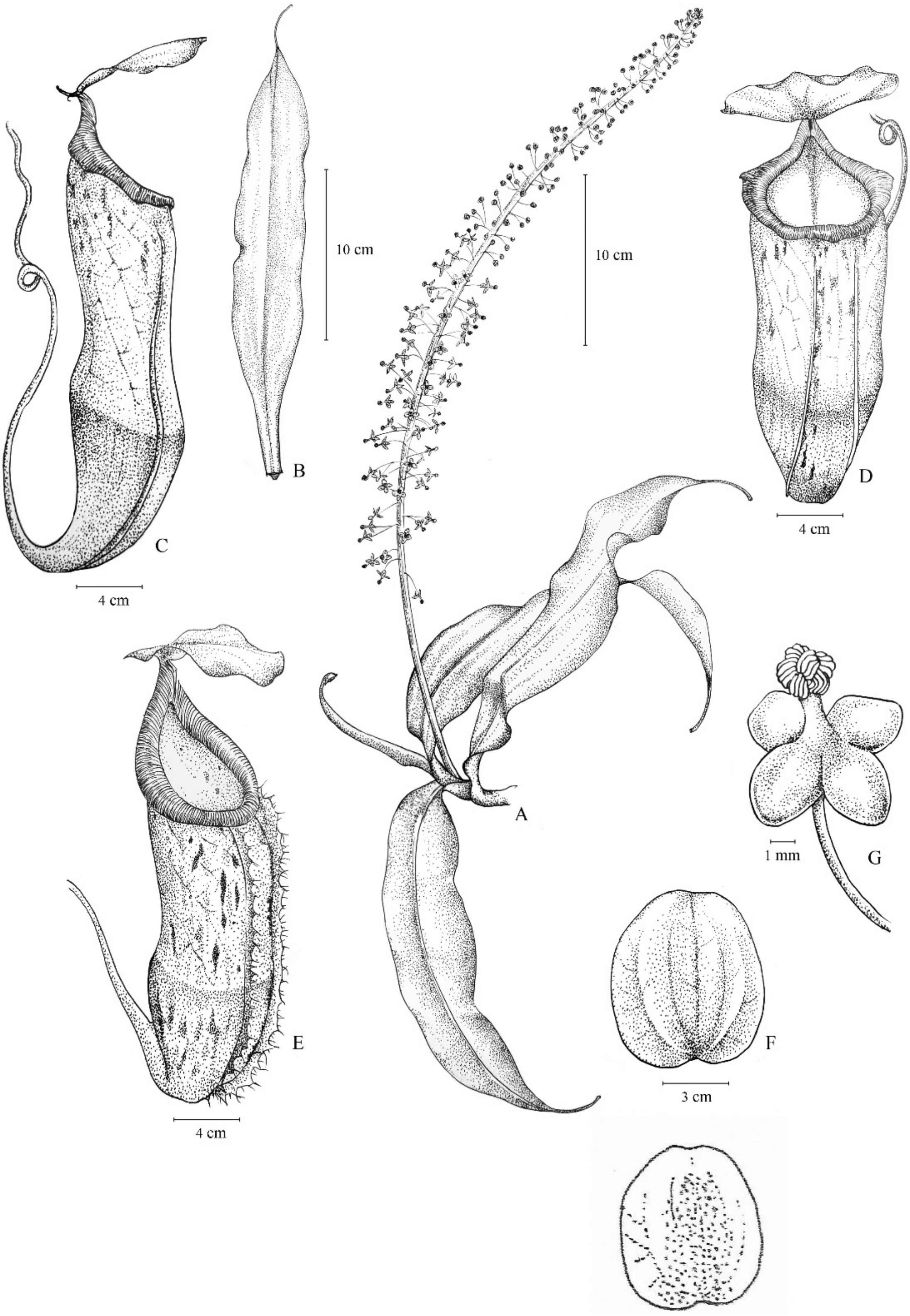

Figure 2. Line drawing of *Nepenthes latiffiana*: **(A)** Habit, with inflorescence. **(B)** Leaf blade. **(C)** Upper pitcher, viewed from side with spur. **(D)** Upper pitcher frontal view. **(E)** Lower pitcher. **(F)** Adaxial and abaxial side of the lid. **(G)** Male flower. Based on 12424 (MDI). All drawn by Khalid Hashim.

Nepenthes domei M. N. Faizal, A. Amin, & A. Latiff, **sp. nov.** (Figures 3 & 4)

Type: Malaysia, Peninsular Malaysia, Terengganu, Setiu, 30 April 2019, MNFG750 (MDI!), MDI12423, *Mohd. Norfaizal, Amin Asyraf, Dome Nikong, Muhamad Ikhwan, Edward Entalai & Anuar Rasyidi* [holotypus, MDI].

Diagnosis

Nepenthes domei differs from *N. benstonei* in several lower pitcher characteristics that include thick-leathery coriaceous texture (vs. coriaceous texture), broad rounded formation in the lower 1/3 or 1/2 part of the lower pitcher (vs. broad ovoid – ovoid in the lower part), two fringed wings 5.5-7 mm wide narrowest at the base and widest at the mouth (vs. less than 4mm runs the whole length of the pitcher body), multicellular fringe elements up to 2-4 mm long (vs. overally shorter, 1-3 mm long). The lower pitchers of the new species frequently burrow into humus, a feature that has not observed in *N. benstonei* from Bukit Bakar. The lower pitchers exhibit whitish red to dark ruby red colouration with the majority of individuals sparsely overlain with or entirely absent of specks on the inner and outer wall (vs. brownish red-dark red, inner wall heavily overlain with specks). The inflorescence rachis length 28-35 cm (vs. less than 30-31 cm). Leaves and stems without waxy cuticle (vs. covered with waxy cuticle).

Description

Terrestrial climber to 3.5 m tall. *Stem and climbing stems* slight rounded in cross section, up to 0.7-0.9 cm in diameter. *Internodes* 4-8 cm on climbing stems and 1.3-2.5 cm on rosette stems. *Leaves* of lower stem coriaceous, lanceolate, sessile, 12-13 cm long and 4-5 cm wide, sheathing the stem up to ¼ of its circumference. Leaf blades of the climbing stems narrowly linear-lanceolate, sessile, 25-32 cm long, 5-8 cm wide, base contracted into the stem up to ½-¾ of the stem, apex narrow acuminate, tendril insertion simple. Longitudinal nerve 1-2 on each side of the midrib, pennate nerves spreading towards the leaf margins. Leaves of climbing stems with slight differentiation to those of the lower stems which is bigger in size. *Tendrils* coiled, up to 13-37 cm long. *Rosette/lower pitchers* up to 15-17 cm long, 4.4-6.5 cm wide; thick-leathery coriaceous texture; arising slight gradually from the tendril; broad rounded formation at the lower part ca. 1/3 with slight pronounced hip, straight cylindrical towards above, widening slightly towards the mouth. Inner surface of the portion below the lid throughout surfaces above the hip smooth and waxiness, light green in colour; two fringed wings up to 7 mm wide (narrowest at the base and widest at the mouth), run from the top of the pitcher to the bottom of the pitcher, consist of multicellular fringe elements up to 2-4 mm long; mouth ovoid-rounded and oblique, concave, rising at the rear of the pitcher towards the lid; peristome slight cylindrical, front up to 6 mm wide, sides up to 4 mm, up to 1.2 cm wide at the rear; outer surface with minute unicellular trichomes, lid ovate, up to 2.7 cm long and 2.4-2.5 cm wide, base generally rounded (not cordate), no hairs or appendages observed on the lower surface. ~60-87 dotted - rounded nectar glands scattered on the lower part of the lid, and concentrated at the base of the lid. *Upper pitchers* 10-12 cm long, 1.5-4 cm wide, thin coriaceous; arising gradually from the tendril; slightly infundibular to cylindrical in the lower part, upper part cylindrical and slight widening towards the mouth; peristome similar to the lower pitchers, differs in mouth shape (wide and length of the mouth and peristome); lid narrow ovate, up to 1.8 cm long and 2.3 cm wide, base rounded (not cordate), no hairs or appendages on the lower surface of the lid; spur simple, unbranched less than 0.5-0.6 cm. *Male inflorescence* a raceme, peduncle up to 13 cm, rachis up to 35 cm, partial peduncles single-flowered, bracts absent, pedicel 11-14 mm long, tepal wide ovate, up to 4-6 mm, staminal column 3-4 mm long, anther head 2-2.5 mm. *Colour of living plants* lower pitcher whitish red to dark ruby red throughout or green-reddish, sometimes with a few red-purple blotches on the inner surfaces and lid, peristome dark red to green with varying degrees of green and red. Leaves and stems without waxy cuticle. Stems reddish-green to green. Leaves dark green. *Colour of dried specimens* dark brown (lamina, stem and pitcher).

Etymology

Named in honour of the first person who discovered the population, Mr. Dome Nikong.

Distribution

Nepenthes domei is currently known only from the restricted area at the type locality in Setiu, Terengganu.

Ecology

Terrestrial climber in humus rich soil, immature and mature lower/rosette pitchers tend to burrow in the soil rich with humus up to 1/3 – 1/2 of the pitcher. Upper hill forest habitats, at an altitude of c. 850-1000 m.

Conservation notes

Nepenthes domei and *N. latiffiana* are terrestrial climbers; with *N. latiffiana* observed growing as understorey

Figure 3. *Nepenthes domei*, in situ: **(A)** Unearthed rosette pitchers with rosette leaves. **(B)** Immature rosette pitcher pulled out from humus rich soil. **(C)** Upper pitcher. **(D)** Lid and inner surface of lower pitchers. **(E)** Leaves from lower stem. **(F)** Rosette/lower pitchers almost entirely buried in the soil. **(G)** Habit, showing stem and leaves. Photographs by Mohd Norfaizal Ghazalli and Amin Asyraf Tamizi.

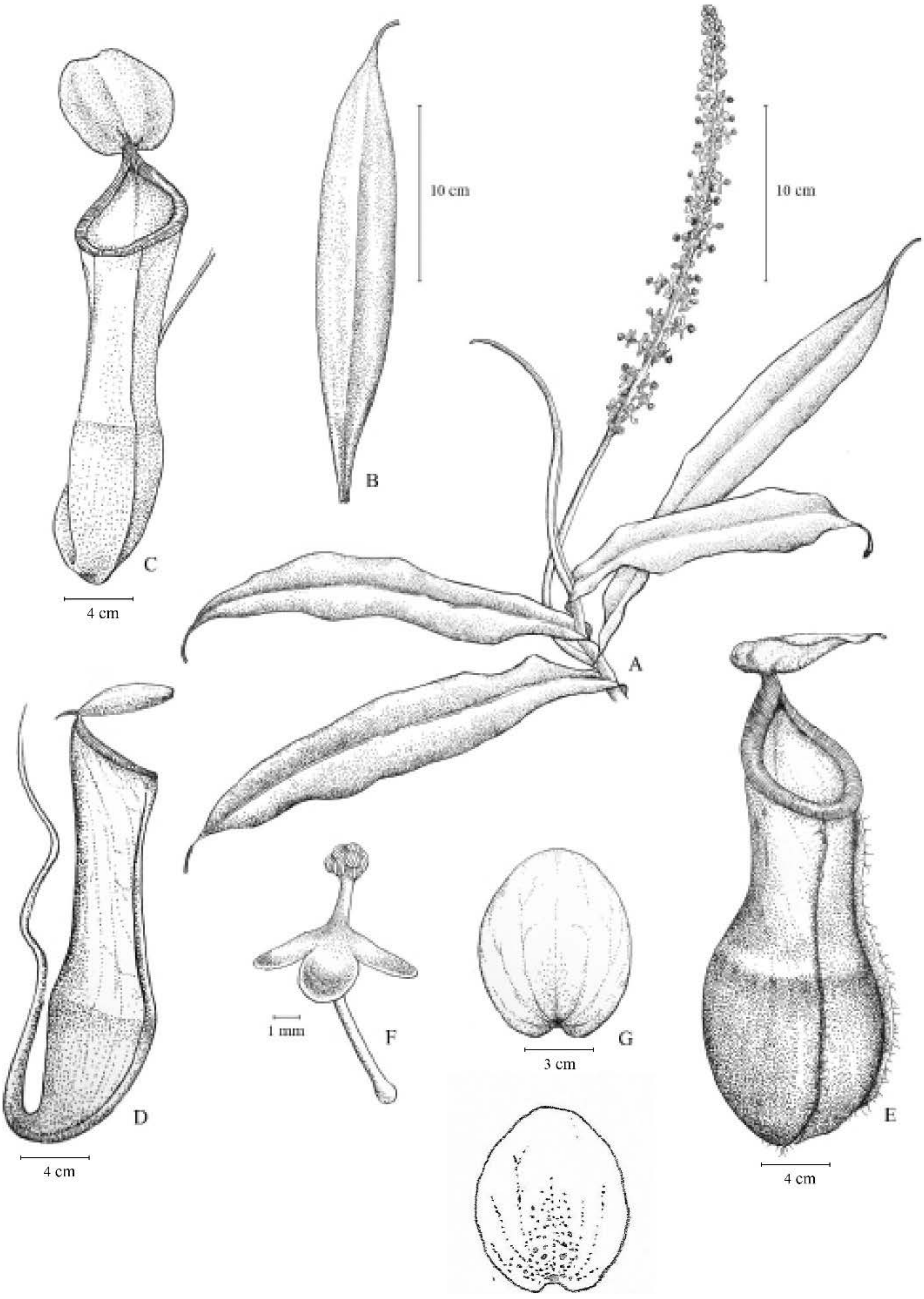

Figure 4. Line drawing of *Nepenthes domei*: **(A)** Habit, with inflorescence. **(B)** Leaf blade. **(C)** Upper pitcher. **(D)** Upper pitcher, viewed from side with spur. **(E)** Lower pitcher. **(F)** Male flower. **(G)** Adaxial and abaxial point view of the lid. Based on 12423 (MDI). All drawn by Khalid Hashim.

plants on a hill slope with rocky substratum at an elevation about c. 1100 m. The vegetation of the locality consisted of various montane species dominated by *Dicranopteris linearis* (Gleicheniaceae), *Dipteris conjugata* (Dipteridaceae) and *Machaerina maingayi* (Cyperaceae), thriving together with rattans, *Pandanus* sp. and *Leptospermum flavescens*. Some climbing stems of *N. domei* were also observed scrambling over *Pandanus* tree. Based on our observation, more than five individuals of *N. domei* were seen at three scattered locations, while only one to two individuals of *N. latiffiana* were recorded at a single location. Both species are known to be restricted in a single mountain since it was discovered. Thus, we assign *N. domei* and *N. latiffiana* in this article as *Vulnerable* under criterion - D2 of IUCN (2001). The habitat had experienced logging in the past; hence, this could explain the limited number of the individuals discovered in the area.

Additional specimens examined

MALAYSIA, Kelantan, Machang, Bukit Bakar, 27.9.2006. *Yao, T.L. et al. FRI53169* (*N. benstonei*); Malaysia, Terengganu, Gunung Tebu, 31.5.1974. *Mohd. Shah et al. FRI13147* (*N. benstonei*); Malaysia, Terengganu, Gunung Padang, 21.3.2010. *Mohd Hairul, M.A. et al. FRI 70887 (N. sanguinea*); Malaysia, Pahang, Cameron Highlands, Ulu Bertam FR, 26.4.2017. *Imin, K. et al. FRI87122* (*N. macfarlanei*).

DISCUSSION AND ADDITIONAL TAXONOMIC NOTES

1) Anatomical descriptions

Nepenthes domei
Holotype: MDI12423

Leaves anatomy lamina thickness 292.48-315.76 µm (Figure 9G), **Hypodermis** 1-3 layers on adaxial, thickness 41.52-55.37 µm, 1 layer on abaxial, thickness 39.56-49.73 µm. Mesophyll 227.38-239.78 µm; palisade parenchyma 1-3 layers with total 157.29-163.21 µm thick; spongy parenchyma total 74.85-89.63 µm, with plenty extracellular space in between of spongy parenchyma (Figure 9G). **Midrib** outline Type I (Figure 9A), 267.89-290.66 µm thick, bigger towards apex leaves; vascular system Type I, sclerenchyma ring not observed, 482.64-515.16 µm diameter, broader towards leaves apex; vascular bundles (8 VB) (Figure 9A & B); 21.28-35.23 µm diameter; midrib epidermis single layer, 11.35-15.45 µm

Table 1. Morphological comparison between *Nepenthes domei, N. latiffiana*, *N.benstonei* and *N. sanguinea* (Figure 1-4).

Character	*N. domei*	*N. latiffiana*	*N. benstonei*	*N. sanguinea*
Altitudinal range	850-1000 m	1000-1100 m	800-1350 m	300-2000 m
Habitat	Terrestrial in rich humus soil, rosette/lower pitchers tend to burrow in the soil up to ½ of the pitcher body.	Terrestrial climber in upper montane forest.	Terrestrial in secondary vegetation and hill slopes.	Terrestrial in shrubland, rocky areas (eg. inland cliffs, mountain peaks), forest/terrestrial.
Tendrils of the rosette and climbing leaves	Slight coiled, up to 13-37 cm long.	With slender coiled formation in the middle; up to 10-14 cm long, covered with minute hairs,	Slightly coiled, less than 60 cm long.	Tendrils slight coiled, less than 30 cm.
Colour of lower pitchers	Whitish red to dark ruby red with a few red-purple blotches on the inner surfaces and lid.	Green-yellowish-brown hues with several red blotches on the 1/3 of the upper part of the pitcher body.	Reddish-brown.	Brown to reddish.
Lid of lower pitchers	Narrow ovate; lid base rounded.	Rounded; lid base retuse-cordate.	Ovate; lid base sub-ovate.	Generally ovate; base usually slight cordate.
Upper pitchers	Up to 10-12 cm high × 1.5-4 cm wide.	Up to 20-23.5 cm high × 5-7.5 cm wide.	Less than 15 cm high × and 3 cm wide.	Less than 35 cm high × less than 7 cm wide.
Colour of upper pitchers	Green.	Light green.	Pale green.	Slight yellowish – green, with several blotches on 1/3 upper part of the pitcher.
Lid of upper pitchers	Narrow ovate to elliptical.	Rounded.	Ovate.	Generally ovate, usually slight cordate at the base.
Colour of dried specimen	Dark brown.	Pale brown.	Brown.	Brown.

at the abaxial and 13.53-20.53 µm at the adaxial, irregular between each other, stomata not observed; trichome or appendages not observed (Figure 9A-F); crystal sand and solitary sand crystals occurring in parenchyma cells of the midrib (Figure 9C & D). **Margin** bluntly pointed below, 75-80 degree pointed below, with epidermis thickness 29.57 µm, margin thickness 139.21 µm, overall blade thickness 291.02-284.75 µm (Figure 9H). **Adaxial epidermis** straight – straight to slightly curve, crystal sand not observed, 2.8-4.5 µm thick; epidermis 1 layer, 2-4 sides, 14.6-29.4 µm × 7.7-27.9 µm; stomata absent; sessile glands rounded up to 7 cells, rounded, trichome absent (Figure 9M). **Abaxial epidermis** straight – straight to slightly curve, 2.2-3.8 µm thick; epidermis 1 layer, irregular, more than 4-5 sides, 17.6-18.3 µm × 5.6-19.5 µm; stomata anomocytic/ranunculaceous (Figure 9L, M & N), sessile glands rounded to flower-like in 7-8 cells, orbicular to elliptical, 42.3-59.6 µm × 40.2-51.8 µm; trichome absent (Figure 9L). **Marginal venation** incomplete type, uni-veinlet (Figure 9I). **Areolar/lamina venation** incomplete (Figure 9J), type of veinlets simple, uni-veinlet (linear-curved) (Figure 9K).

Nepenthes latiffiana
Holotype: MDI12424

Leaves anatomy lamina thickness 788.68 -794.50 µm (Figure 10E & H), **Hypodermis** 1-2 layers on adaxial, thickness 152.89-162.33 µm, 1 layer on abaxial. Mesophyll 296.56-390.76 µm; palisade parenchyma 2-3 layers 342.44-387.64 µm thick; spongy parenchyma 564.59-576.54 µm, with plenty extracellular space in between of spongy parenchyma (Figure 10F & H). **Midrib** outline Type IV, adaxial with slightly flat and abaxial prominent broad 'U' curve (Figure 10A), 669.63-689.45 µm thick, smaller towards apex leaves; vascular system Type VI, schlerenchyma ring orbicular upwards, slightly curved at adaxial, outer ring present, central or medullary vascular bundle present (3 VB), additional vascular bundle present (several smaller size vascular bundles observed near abaxial epidermis, 380.23-395.56 µm diameter (Figure 10A-D); up to 50.67 µm diameter; irregular between each other; stomata not observed; trichome appendages not observed (Figure 10A); crystal sand - miniature solitary crystals occurring in parenchyma cells of the midrib (Figure 10B & D). **Margin** sharp pointed pointed below up to 85 degree, with epidermis thickness 13.35-21.58 µm, margin thickness 136.78-146.75 µm, overall blade thickness 335.65-380.76 µm (Figure 10F). **Adaxial epidermis** straight – straight to curve, druses observed on the adaxial surface, 3.7-6.5 µm thick; epidermis 1 layer, 4-5 sides, 15.1-38.7 µm × 5.9-22.3 µm; stomata absent; sessile glands irregular in rounded up to 6 cells, elliptical-orbicular, trichome absent (Figure 10L). **Abaxial epidermis** straight – straight to curve, 2.4-4.1 µm thick; epidermis 1 layer, irregular, more than 4 sides, 14.32-28.54 µm × 43.5-32.6 µm; stomata anomocytic/ranunculaceous (Figure 10M &N), rounded, 108.25-122.645 µm × 118.1-119.4 µm, sessile glands not observed, trichome absent. **Marginal venation** closed type, none veinlet (Figure 10K). **Areolar/lamina venation** incomplete (Figure 10I), type of veinlets simple uni-bi veinlet (curved) (Figure 10J).

Nepenthes benstonei

Leaves anatomy lamina thickness 252.96-266.43 µm (Figure 11G), **Hypodermis** 1-2 layers on adaxial, thickness 25.67-35.94 µm, 1 layer on abaxial, thickness 16.26-27.38 µm. Mesophyll 159.17-172.86 µm; palisade parenchyma 1-3 layers with total 67.65-84.15 µm thick; spongy parenchyma total 106.97-111.25 µm, with plenty extracellular space in between of spongy parenchyma (Figure 11G & H). **Midrib** outline Type I, adaxial very slightly concave, abaxial prominent 'U-V' Shape (Figure 11A), 380.81-391.71 µm thick, vascular system Type VI, outer ring present (rectangular in shape), central vascular bundle present (3 vascular bundles), additional vascular bundle present (several smaller size vascular bundle near abaxial epidermis) and 2 vascular bundle present on the adaxial side of outer ring vascular bundle at the left and right side, midrib epidermis single layered, 13.26-17.83 µm at the abaxial and 15.59-16.42 µm at the adaxial, irregular between each other; stomata not observed; trichome appendages not observed (Figure 11A & I); crystal sand - solitary sand crystals occurring in masses specifically in parenchyma cells of the midrib (Figure 11B-D), druses observed (Figure 11E), starch grains observed. (Figure 11B). **Margin** sharply pointed below 20-25 degree, with epidermis thickness 8.81-13.25 µm, margin thickness 68.51-82.83 µm (Figure 11H). **Adaxial epidermis** straight to wavy, crystal sand observed on the adaxial surface, 3.5-4.9 µm thick; epidermis 1 layer, 4-6 sides, 15.6-34.5 µm × 8.4-9.3 µm; stomata absent; sessile glands irregular in flower-like in 6-7 cells, elliptical, trichome absent (Figure 11J). **Abaxial epidermis** sinuous, 2.5-3.8 µm thick; epidermis 1 layer, irregular, more than 4 sides, 18.42.87 µm x 6.5-36.9 µm; stomata anomocytic/ranunculaceous (Figure 11K), kidney-like, trichome absent. **Marginal venation** closed type, none veinlet (Figure 11M). **Areolar/lamina venation** incomplete (Figure 11L), type of veinlets simple veinlet (linear-curved) 1-2 branched (Figure 11L).

Nepenthes sanguinea

Leaves anatomy lamina thickness 224.20-235.23 µm (Figure 12E), **Hypodermis** 1 layer on adaxial, thickness 20.54-37.65 µm, 1 layer on abaxial, thickness 29.15-32.52 µm. Mesophyll 145.87-166.45 µm; palisade parenchyma 2 layer with total 53.06-63.32 µm thick; spongy parenchyma total 90.71-94.99 µm, with plenty extracellular space in between of spongy parenchyma (Figure 12E & F). **Midrib** outline Type I, adaxial slightly flattened and abaxial arched, (Figure 7a), 383.37-445.89 µm thick, vascular system Type VI, sclerenchyma ring orbicular upwards, slightly curved at adaxial, outer ring present, central or medullary vascular bundle present (4 VB), 1 additional vascular bundle present (smaller size vascular bundles observed near abaxial epidermis), 367.11-413.32 µm diameter (Figure 7A-C); diameter up to 40.35 µm; irregular between each other; stomata not observed; trichome appendages not observed (Figure 12A); crystal sand - solitary crystals and druse occurring in parenchyma cells of the midrib (Figure 12B-D). **Margin** sharp tip pointed below up to up to 80 degree, roughly crease surface, with epidermis thickness 6.85-9.41 µm, margin thickness 86.76-92.23 µm, overall blade thickness 89.05-106.97 µm (Figure 12F). **Adaxial epidermis** straight – slight curve, druses not observed on the adaxial surface, 3.8-7.8 µm thick; epidermis 1 layer, 3-5 sides; stomata absent; sessile glands irregular in rounded up to 5 cells, elliptical, trichome absent (Figure 12I). **Abaxial epidermis** straight – slight curve, 2.4-4.9 µm thick; epidermis 1 layer, irregular, more than 4-6 sides; stomata anomocytic (Figure 12J), 95.47-117.74 µm × 105.54-147.65 µm, sessile glands not observed, trichome absent. **Marginal venation** incomplete type, uni-veinlet (Figure 12H). **Areolar/lamina venation** incomplete (Figure 12I), type of veinlets – simple uni veinlet (slight curved) (Figure 12I).

Table 2. Comparison of leaf micromorphological observation between *Nepenthes domei*, *N. latiffiana*, *N. benstonei* and *N. sanguinea* (Figure 5-8).

	N. domei	*N. latiffiana*	*N. benstonei*	*N. sanguinea*
Cuticular striation	**Adaxial:** smooth-coarse; anticlinal wall not clear; periclinal wall sunken, cuticular striation not obscure and both anticlinal and periclinal walls cannot be differentiated clearly. Epidermal cell outline obscured by appendages. **Abaxial:** smooth surface, with granular waxes; both anticlinal and periclinal walls cannot be differentiated clearly.	**Adaxial:** coarse; anticlinal wall clear; periclinal wall sunken, cuticular striation obscure and both anticlinal and periclinal walls cannot be differentiated clearly. Epidermal cell outline obscured by high density of waxes. **Abaxial:** coarse; with granules waxes; both anticlinal and periclinal walls can be differentiated clearly.	**Adaxial:** coarse; anticlinal wall not clear; periclinal wall sunken, cuticular striation obscure and both anticlinal and periclinal walls can be differentiated. Epidermal cell outline obscured by high density of waxes. **Abaxial:** coarse; with flaked waxes; both anticlinal and periclinal walls cannot be differentiated clearly due to high density of flakes and appendages.	**Adaxial:** coarse; anticlinal wall not clear; periclinal wall sunken, both anticlinal and periclinal walls can be differentiated clearly. Epidermal cell outline not obscured by high density of waxes. **Abaxial:** medium coarse; both anticlinal and periclinal walls can be differentiated.
Epicuticular waxes	i. Granules present on both adaxial and abaxial surfaces, tubular wax on abaxial.	i. Flakes (adaxial) ii. Granules (abaxial)	i. Flakes (adaxial) ii) Granules (abaxial)	Flakes present on both adaxial and abaxial epidermises.
Stomata features	Amphistomatous, sunken, scattered mainly on the abaxial surface, sparsely distributed on the adaxial surface, rounded shape.	Hypostomatic, superficial, restricted to and sparsely scattered on the abaxial epidermis surface, broad oval shape.	Hypostomatic, superficial, restricted to and sparsely scattered on the abaxial epidermis surface, broad oval shape.	Amphistomatous, sunken, scattered mainly on the abaxial surface, sparsely distributed on the adaxial surface, rounded-oval shape.
Types of trichomes	**i.** Simple unicellular (long, pointed tip, with slight echinate ornamentation). **ii.** Capitate glandular trichome (multicellular terminal). **iii.** Capitate glandular trichome (unicellular terminal). **iv.** Peltate, Scale trichome.	**i.** Simple unicellular (long, pointed tip, slight echinate ornamentation. **ii.** Simple unicellular short, blunt tip, without echinate ornamentation **iii.** Capitate glandular trichome (multicellular terminal).	**i.** Simple unicellular (long, pointed tip, smooth). **ii.** Capitate glandular trichome (unicellular terminal). **iii**. Capitate glandular trichome (multicellular terminal).	**i.** Capitate glandular trichome (multicellular terminal).

Table 3. Comparison of leaf anatomical features between *Nepenthes domei*, *N. latiffiana, N. benstonei* and *N. sanguinea* (Figure 9-12).

	N. domei	*N. latiffiana*	*N. benstonei*	*N. sanguinea*
Leaf margin	Bluntly pointed below 75-80°.	Sharply pointed below up to 85°.	Sharply pointed below 20-25°.	Sharply pointed below up to up to 80°, with roughly crease surface.
Midrib	Outline Type I.	Outline Type IV.	Outline Type I.	Outline Type I.
Vascular bundle arrangement	Arrangement Type I.	Arrangement Type VI.	Arrangement Type VI.	Arrangement Type VI.
Marginal venation	Incomplete type, uni-veinlet.	Closed type, none veinlet.	Closed type, none veinlet.	Incomplete type, uni-veinlet.
Areolar venation	Incomplete, type of veinlets simple, uni-veinlet (linear-curved).	Incomplete, type of veinlets simple uni-bi veinlet (curved).	Incomplete; type of veinlets simple veinlet (linear-curved) 1-3 branched.	Incomplete, type of veinlets-simple uni-veinlet (slightly curved).
Pattern of anticlinal cells	**Adaxial:** straight – straight to slightly curved. **Abaxial:** straight – straight to slightly curved.	**Adaxial:** straight – straight to curved. **Abaxial:** straight – straight to curved.	**Adaxial**: straight to wavy, crystal sand observed on the adaxial surface. **Abaxial:** sinuous.	**Adaxial:** straight –slightly curved. **Abaxial:** straight – slightly curved.
Stomata feature	Anomocytic (type of stomata-without subsidiary cells); Homostomatic (only one type of stomata present); Amphistomatous (stomata present on both epidermis surfaces).	Anomocytic; Homostomatic; Hypostomatic (stomata only present on abaxial epidermis).	Anomocytic; Homostomatic; Hypostomatic.	Anomocytic; Homostomatic; Amphistomatous.

Results of the study revealed a number of interesting features with some characters which could serve as taxonomic and diagnostic value, while assist in giving additional evidences in describing *N. domei* and *N. latiffiana* against related species. Anatomical diagnostic characters that can be used in directly differentiating and possessed taxonomic value are sclerenchyma ring type and shape, and marginal venation and lamina venation that enumerate significant taxon separation between *N. domei* and *N. benstonei*, and *N. latiffiana* and *N. sanguinea*. Supportive micromorphology and anatomy characters which are also useful in assisting these taxa identification (diagnostic characters) in new taxon descriptions are noted as below, with identification key of the species:

2) Diagnostic characters of Nepenthes domei and N. latiffiana based on leaf anatomy and micromorphology

Anticlinal walls of lamina epidermal cells under light microsope (LM)

According to Stace (1969), the lamina surface has been the focal subject of investigations (as compared with other plant surfaces) that some of studied taxa showed consistent characteristics which often serve as a taxonomic application. From observations of the lamina surface in studied *Nepenthes*, the anticlinal wall of *N. domei* is straight to slight curve for both abaxial and adaxial epidermis surfaces while *N. benstonei* showed straight to wavy adaxial epidermis surface and sinuous abaxial epidermis surface. On the other hand, *N. latiffiana* showed straight to straight curve epidermis wall for both of its surfaces as compared to *N. sanguinea* which possessed straight – slightly curve and straight for its abaxial epidermis. Therefore, these characters appear to be diagnostic for those two new species, respectively.

Margin and Midrib Transverse Section (TS)

Studied *Nepenthes* species showed interspecies variations in lamina margin transverse section (TS) which can serve as a useful characteristic for species identification. The outline of the TS of the margin is bluntly rounded (pointed 75-80°) for *N. domei*, sharply pointed downwards that reached 85° for *N. latiffiana*, sharply pointed with 20-25° curve for *N. benstonei*, while *N. sanguinea* having up to 80° and rough creased abaxial and adaxial surfaces. Midrib outline for *N. domei*, *N. sanguinea* and *N. benstonei* is characterised as **Type I** (abaxial with prominent U-V shape and adaxial with very slight concave shape) while *N. latiffiana* having **Type IV** (abaxial with prominent V shape and adaxial with prominent wide V shape) midrib outline. For midrib TS, the variations are as follows: *N. domei* is having **Type I** (adaxial vascular bundle in stacks, medullary vascular bundle absent, additional vascular bundle present in several smaller size nearby the abaxial epidermis) vascular bundle arrangement, while *N. latiffiana*, *N. benstonei* and *N. sanguinea* are having **Type VI** vascular bundle arrangement (outer ring present, elliptic; central medullary vascular bundle present in scattered formation; additional vascular bundle present in several smaller size nearby the adaxial side of outer ring at the left and right side). These observations (disparity in vascular bundle arrangement combined with midrib outline) agree with some studies conducted by Metcalfe and Chalk (1950) who demonstrated the two characteristics could greatly serve for diagnosis in certain species, as recorded and showed in some Parashorea species.

Marginal and areolar venation

The variation of leaf venation patterns of angiosperms was extensively studied and classified by Hickey (1979) and Sun et al. (1997) and this further addresses the importance of comprehensive treatment in taxon differentiation. Leaf architecture is primarily used for classification which includes the leaf shape, leaf margin structure and other possible characters. Indeed, the characterisation of an angiosperm leaf venation pattern starts by observing the primary veins and then proceeded to the branching secondary veins. Combination of marginal venation and areolar venation patterns for every taxon are unique, even for those taxa classified under the same genus (Inamdar et al. 1983). In studied *Nepenthes* species, marginal and lamina/areolar venation features showed diagnostic characteristics that are useful in species differentiation and evaluation. *Nepenthes domei* and *N. sanguinea* showed incomplete univeinlet, while *N. benstonei* and *N. latiffiana* are characterised with closed type, with none veinlet. Another feature analysed is the areolar / lamina venation, in which all taxa showed incomplete areolar venation but varied in type of venation ending as follows: *N. domei* showed simple veinlet with uni-veinlet (linear to curved), while *N. latiffiana* and *N. benstonei* shared the same feature of uni-bi veinlet (curved) that slightly differs in *N. benstonei* venation ending with linear-curved (1-3 branched) and *N. sanguinea* characterised with uni-veinlet (slight curved). These variable patterns of leaf venation are taxonomically significant in these pitcher plants species as they can be used as additional evidences for species differentiation.

Cuticular wax and epidermal sculpturing under scanning electron microscopy (SEM)

Cuticular sculpturing also holds considerable diagnostic values as reported by Wilkinson (1979) and Wu et al. (2005). In this study, the epidermal surfaces revealed a number of important micromorphological characters, exhibited interesting interspecies variations that are significant for species identification. Leaf epidermis surfaces (abaxial and adaxial) of the investigated *Nepenthes* species that were viewed under the SEM (low to high magnifications) gave certain features – distribution of idioblastic elements such as trichomes, glands and stomata, combined with the appearance of epicuticular wax. In this study, the appearance of epicuticular wax on both of the leaf surfaces could be tubular granular or flaked, or a combination of different types of wax. *Nepenthes domei* differed from others for having granular wax on both abaxial and adaxial epidermis surfaces, and tubular wax only on abaxial surface (Figure 5). Meanwhile its closely related species, *N. benstonei*, showed numerous wax flakes (Figure 7) for its adaxial epidermis surface and granules for its abaxial surface. It seems the presence of these numerous flakes supports Clarke's (2001) observation saying that the leaves and stems of *N. benstonei* were covered with thick waxy cuticle. *Nepenthes latiffiana* showed similar features as that of *N. benstonei*, while *N. sanguinea* had wax flakes on both abaxial and adaxial surfaces. Stomata features also implicate a significant diagnostic value for our species of interest. *Nepenthes domei and N. sanguinea* leaves are amphistomatous (stomata on both surfaces); however *N. benstonei* and *N. latiffiana* are hypostomatous (stomata only on the lower surface). While hypostomatous stomata feature is common for the majority of species for monocotyledons and dicotyledons (Meidner and Mansfield 1968), amphostomatous feature is much rare (Drake et al., 2018). Drake et al. (2018) further points out that amphistomaty may help in better CO2 absorption but with higher rate of transpiration and this discovery of two different groups of leaves (hypostomatous vs. amphostomatous) within the same genus is truly intriguing. The indumentum feature in dicotyledons was reported to consist of simple unicellular and various glandular trichomes (Metcalfe and Chalk, 1950). In this study, glandular trichomes was present in all species but *N. domei* showed diagnostic character with the observation of scale-type trichomes, known as peltate, on its abaxial epidermis surface that did not exist in other investigated species. Simple unicellular trichomes are common and present in all species of studied *Nepenthes* except in *N sanguinea* that also can be postulated as a diagnostic characteristic that differentiates *N. latiffiana* from *N. sanguinea*. This trichome type can be long or short, and has either thick wall ornamentation or smooth.

Identification key based on anatomy and micromorphology characters

1 a. Midrib outline Type I; vascular bundle arrangement Type I, with peltate trichome.................................***N. domei***

b. Midrib outline Type IV; vascular bundle arrangement type VI..2

2 a. Margin transverse section sharply pointed over 20-25° 3

b. Margin transverse section sharply pointed below up to 85° ....***N. latiffiana***

3 a. Adaxial epidermal cell outline obscured by high density of waxes...***N. benstonei***

b. Adaxial epidermal cell outline not obscured by high density of waxes...4

4 Simple unicellular trichome absent, only peltate glandular trichome (multicellular terminal) observed ...***N. sanguinea***

3) Molecular analysis of ITS sequence to infer the relationship between N. benstonei and other species

The ITS is a nuclear DNA region which is highly conserved and it has been used successfully to discriminate different plant species including *Nepenthes* (Giudicelli et al. 2015; Gogoi and Bhau 2018). Based on nucleotide search on the public NCBI database (BLASTn), we noted partial ITS region (~610bp) is more than 95% conserved among the majority species in the *Nepenthes* genus and the ITS may not be sensitive to differentiate sub-populations under the same species. However, we tested the degree of ITS sequence conservation from a few different populations of *N. sanguinea* in Peninsular Malaysia and it is proven the partial ITS sequence is 100% conserved within this particular species (data not shown), saying that ITS intraspecific variation of a closed population should be close to 0.

In order to further establish *N. domei* as a separate taxon from its most closely related species *N. benstonei*, we conducted a molecular analysis by comparing the partial ITS sequence from both plants (Figure 13) and then inferred phylogenetic relationship (NJ method) of the new species with nine peninsular *Nepenthes* species (Figure 14). Based on sequence alignment, *N. domei* sp. nov shares up to 97.2% ITS nucleotide identity to *N. benstonei*, and the 2.8% nucleotide dissimilarity – a figure significant enough to differentiate *Nepenthes* species in this study – is due to nucleotide polymorphisms that occur at 15 different positions, denoted as non-coloured letters (Figure 13). In addition to this, the phylogenetic inferring has positioned *N. domei* on a separate branch from *N. benstonei* in the highland/intermediate highland clade (Figure 14). This molecular scrutiny – on top of morphology, leaf anatomy and micromorphology – serves as an addition evidence that has positioned *N. domei* as a distinct species from *N. benstonei*.

CONCLUSION

The combination approach of morphology-anatomy-micromorphology analyses used in this comparison study is useful in providing as much aspects as possible in distinguishing plant characteristics of *N. domei* and *N. latiffiana* against their congener species, *N. benstonei* and *N. sanguinea*. As a whole, pitcher morphology of both new species combined with detailed descriptions of the midrib, lamina and epidermis have addressed comprehensive taxonomic resolution in defining these new *Nepenthes* species. Also, the phylogenetic inference has provided an additional supportive evidence for the placement of *N. domei* as a new species. Hence, *N. domei* and *N. latiffiana* described in this paper are confidently positioned as two new species discovered from eastern part of Peninsular Malaysia.

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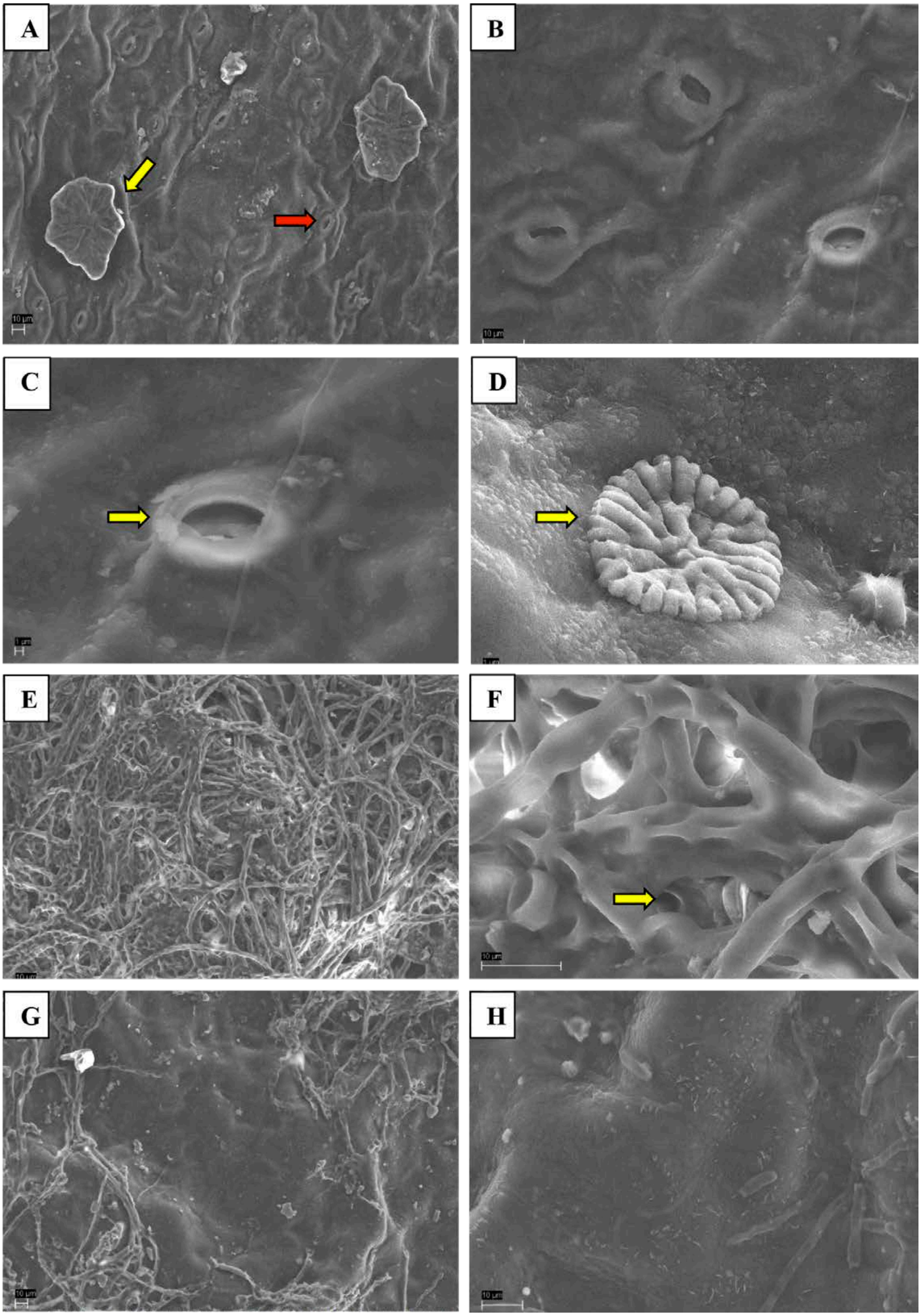


Figure 5. *Nepenthes domei*: (**A**) Abaxial epidermis; stoma (red arrow) and peltate trichome (yellow arrow). (**B**) Stomata and epicuticular wax. (**C**) Stoma (arrow). (**D**) Peltate (scale) trichome. (**E**) Adaxial epidermis with tubular wax. (**F**) Stoma deep embedded into tubular wax (arrow) observed on the adaxial epidermis. (**G**) Granular wax mixed with tubular. (**H**) Cuticular striation. SEM images by by Mohd Norfaizal Ghazalli and Ahmad Zaki Zaini.

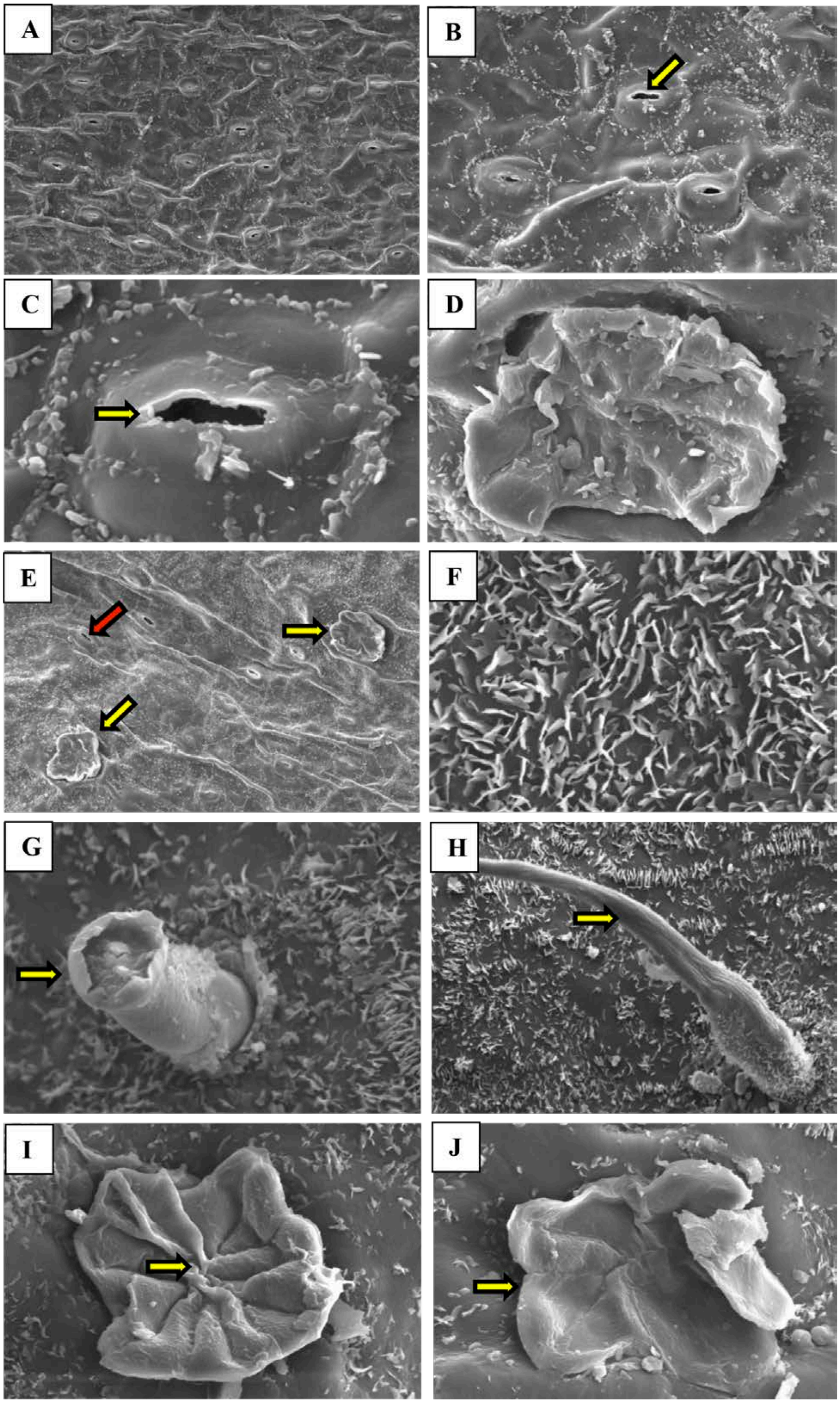


Figure 6. *Nepenthes latiffiana*: **(A)** Abaxial epidermis adorned with numerous stomata. **(B)** Abaxial stomata (arrow). **(C)** Stomata (arrow) on abaxial surface with wax granules. **(D)** Peltate glandular trichome. **(E)** Peltate glandular trichomes (yellow arrows) and stoma (red arrow). **(F)** Adaxial epidermis with wax flakes but without stomata. **(G)** Capitate glandular trichome (arrow). **(H)** Simple, unicellular trichome, long pointed (arrow). **(I & J)** Variation of multicellular peltate glandular trichome (arrow). SEM images by Mohd Norfaizal Ghazalli and Ahmad Zaki Zaini.

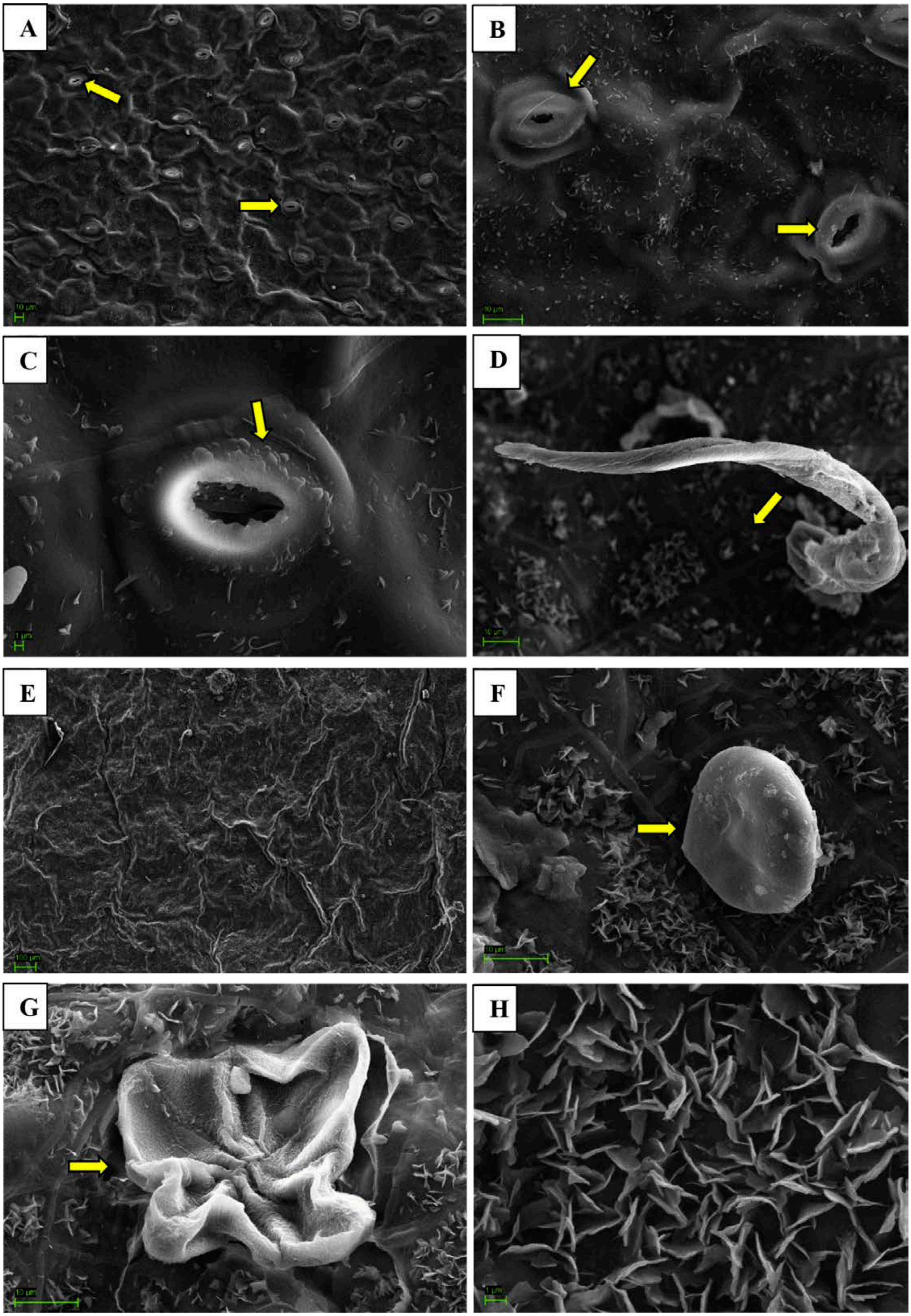


Figure 7. *Nepenthes benstonei*: **(A & B)** Abaxial epidermis with stomata (arrows). **(C)** Abaxial stoma surrounded by wax granules (arrow). **(D)** Simple, unicellular trichome, long pointed (arrow). **(E)** Adaxial surface absent of stomata. **(F)** Capitate glandular trichome (arrow) surrounded by wax flakes. **(G)** Multicellular peltate glandular trichome (arrow). **(H)** Flakes observed on the adaxial epidermis. SEM images by Mohd Norfaizal Ghazalli and Ahmad Zaki Zaini.

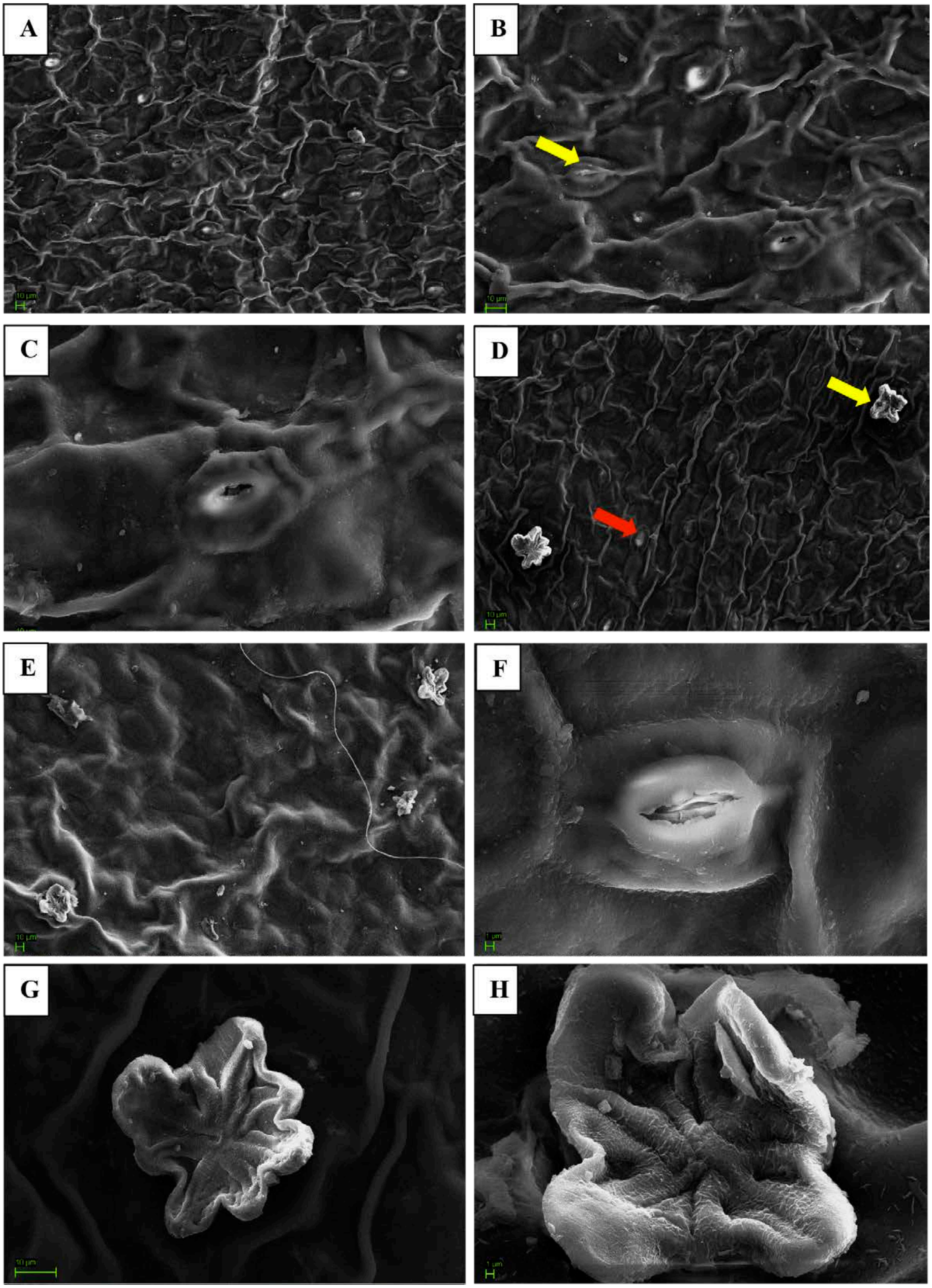


Figure 8. *Nepenthes sanguinea*: **(A)** Abaxial epidermis. **(B)** Stomata (arrow). **(C)** Stoma. **(D)** Adaxial epidermis with stoma (red arrow) and peltate glandular trichome (yellow arrow). **(E)** Adaxial epidermis surface. **(F)** Stoma. **(G & H)** Variation of multicellular peltate glandular trichomes observed on the adaxial epidermis surface. SEM images by by Mohd Norfaizal Ghazalli and Ahmad Zaki Zaini.

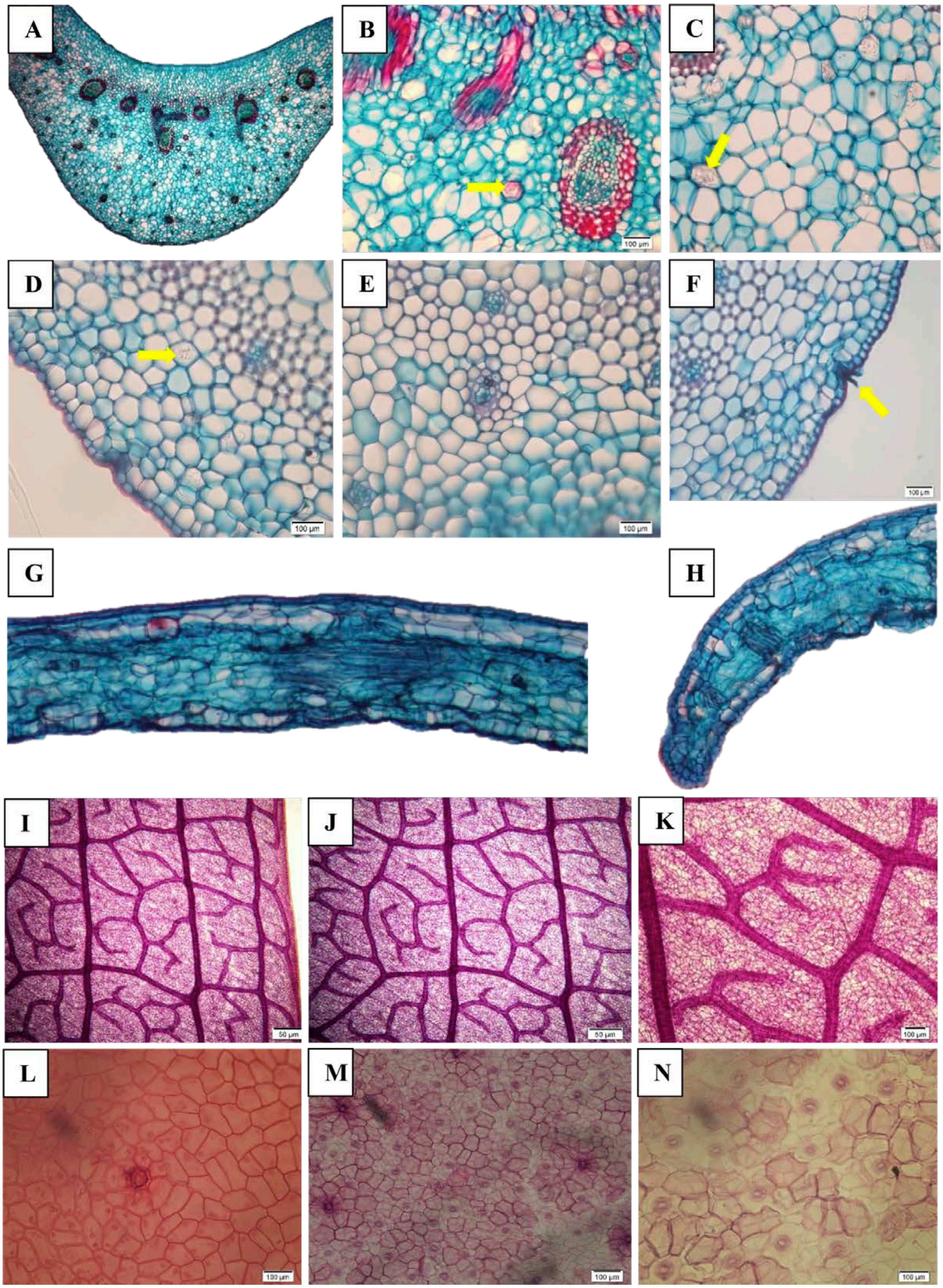


Figure 9. *Nepenthes domei*: (**A**) Midrib TS. **(B, C & D)** Solitary sand crystal (arrows). **(E)** Parenchyma cells. **(F)** Simple, unicellular trichome (arrow). **(G)** Lamina TS**. (H)** Margin TS. **(I)** Margin venation. **(J)** Lamina venation. **(K)** Type of veinlet. **(L)** Adaxial epidermis showing a stoma. **(M & N)** Abaxial epidermis with stomata. Photographs by Mohd Norfaizal Ghazalli and Amin Asyraf Tamizi.

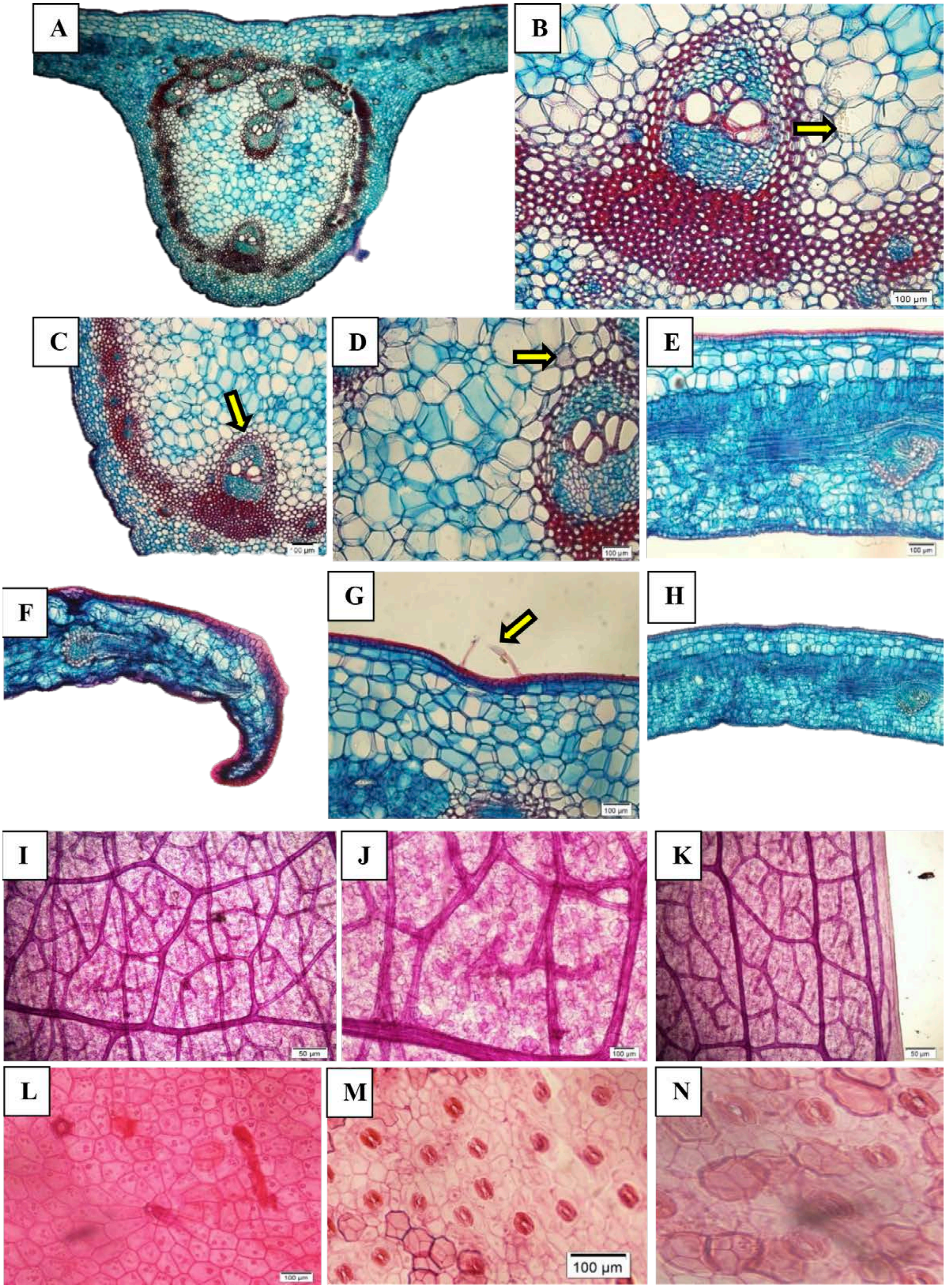


Figure 10. *Nepenthes latiffiana:* **(A)** Midrib TS. **(B)** Solitary crystal (arrow). **(C)** Vascular bundle (arrow). **(D)** Solitary sand crystal. **(E)** Lamina TS. **(F)** Margin TS. **(G)** Simple, unicellular trichomes (arrow). **(H)** Lamina TS. **(I)** Lamina venation. **(J)** Type of veinlet. **(K)** Margin venation. **(L)** Adaxial epidermis. **(M)** Abaxial epidermis with stomata. **(N)** Stomata. Photographs by Mohd Norfaizal Ghazalli and Amin Asyraf Tamizi.

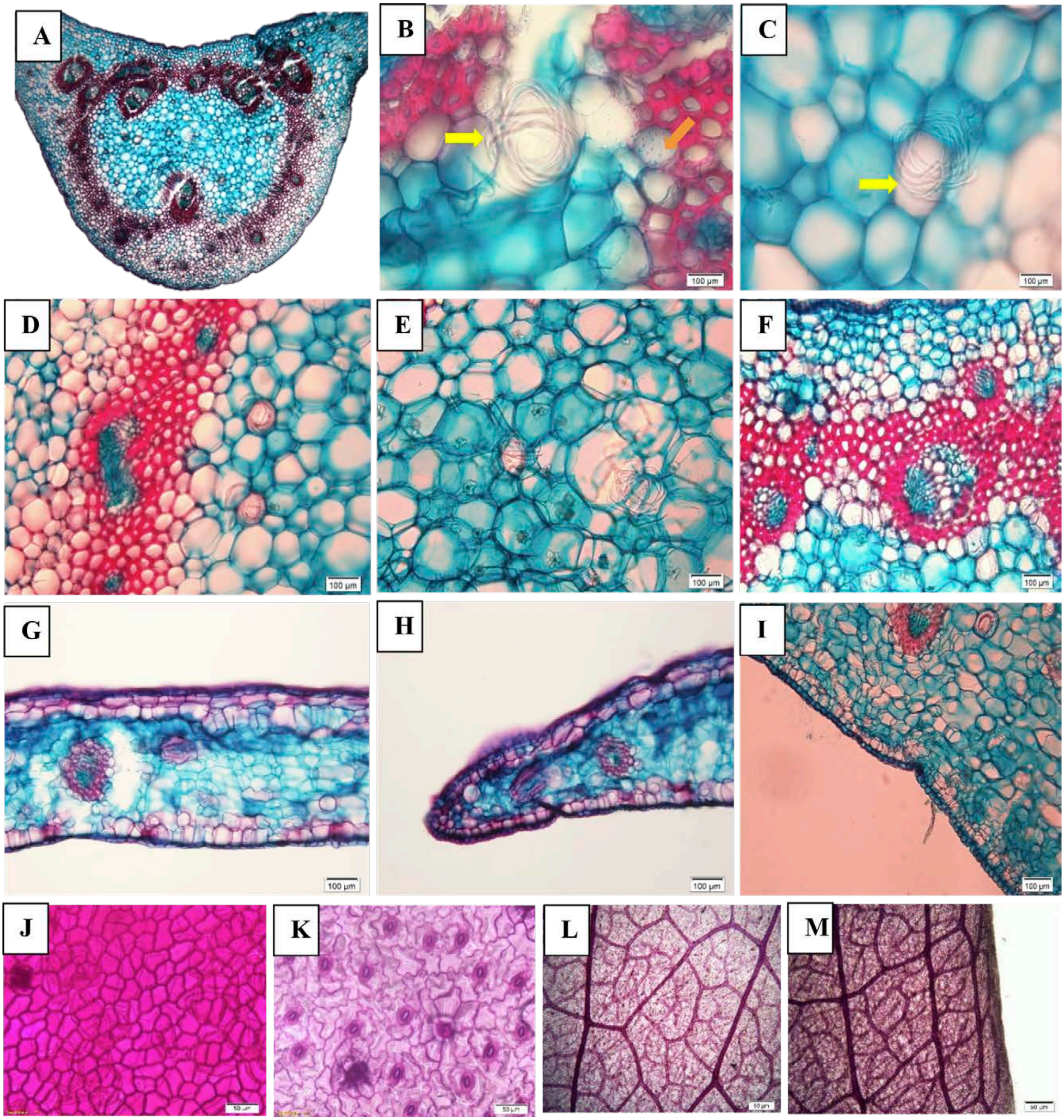


Figure 11. *Nepenthes benstonei*: **(A)** Midrib TS. **(B)** Observation of solitary crystal (yellow arrow) and starch grain (orange arrow). **(C)** Solitary crystal (arrow). **(D)** Solitary crystal. **(E)** Druses. **(F)** Vascular bundle. **(G)** Lamina TS. **(H)** Margin TS. **(I)** Simple, unicellular trichome. **(J)** Adaxial epidermis. **(K)** Abaxial epidermis with stomata observation. **(L)** Lamina venation. **(M)** Margin venation. Photographs by Mohd Norfaizal Ghazalli and Amin Asyraf Tamizi.

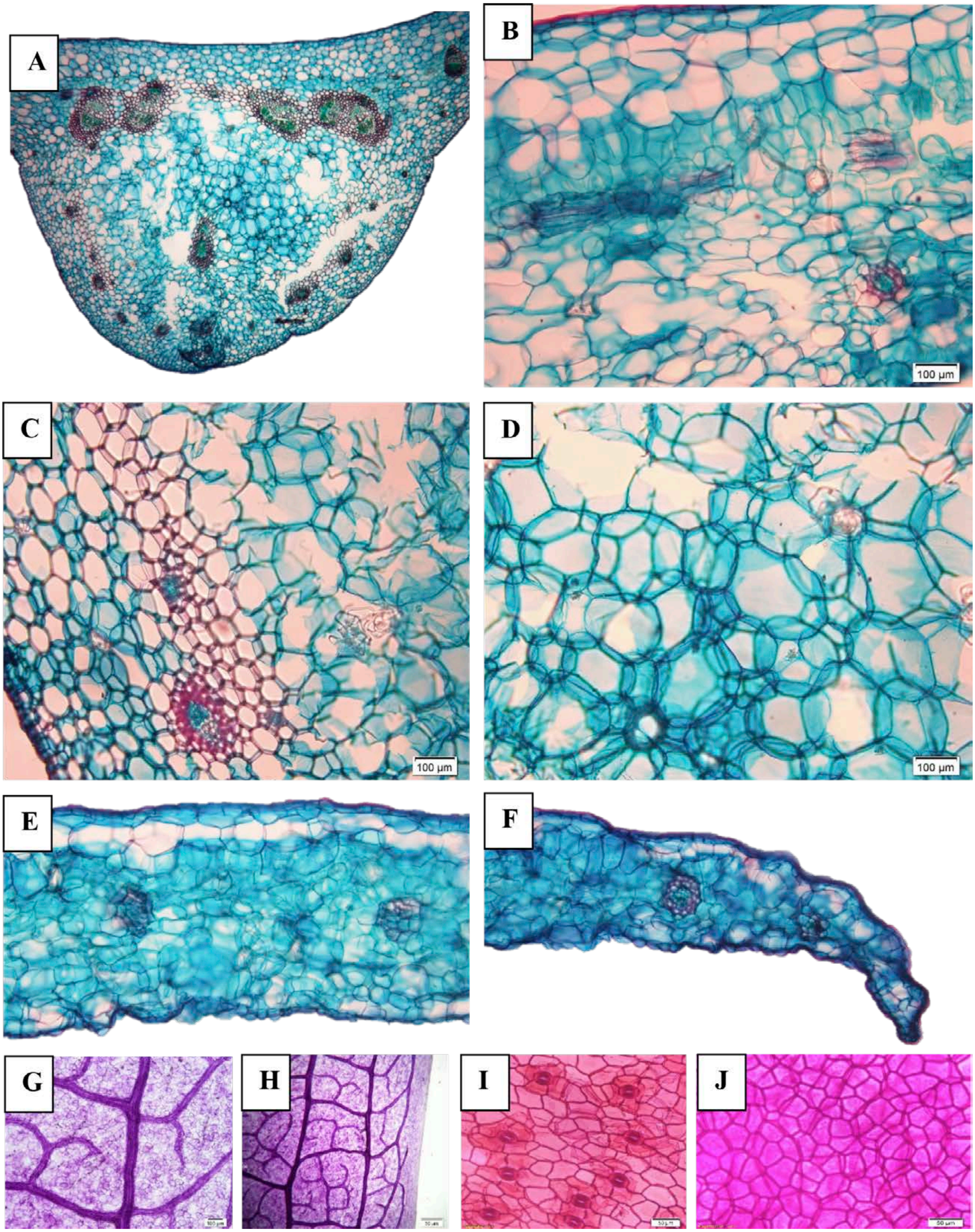
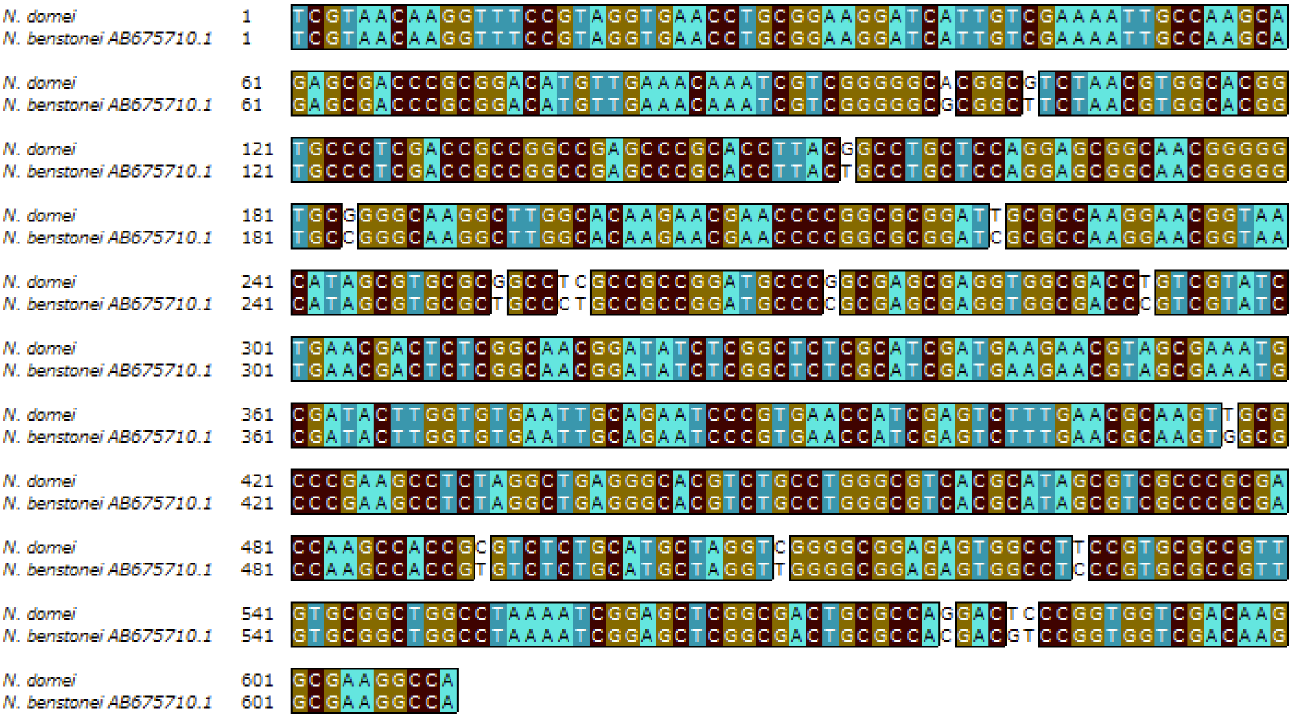


Figure 12. *Nepenthes sanguinea*: **(A)** Midrib TS. **(B)** Solitary crystal (arrow). **(C)** Solitary crystal (arrow). **(D)** Solitary sand crystal. **(E)** Lamina TS. **(F)** Margin TS. **(G)** Lamina venation. **(H)** Marginal venation. **(I)** Abaxial epidermis. **(J)** Adaxial epidermis. Photographs by Mohd Norfaizal Ghazalli and Amin Asyraf Tamizi.



```
N. domei                  1  TCGTAACAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTGTCGAAAATTGCCAAGCA
N. benstonei AB675710.1   1  TCGTAACAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTGTCGAAAATTGCCAAGCA

N. domei                 61  GAGCGACCCGCGGACATGTTGAAACAAATCGTCGGGGGCACGGCGTCTAACGTGGCACGG
N. benstonei AB675710.1  61  GAGCGACCCGCGGACATGTTGAAACAAATCGTCGGGGGCGCGGCTTCTAACGTGGCACGG

N. domei                121  TGCCCTCGACCGCCGGCCGAGCCCGCACCTTACGGCCTGCTCCAGGAGCGGCAACGGGGG
N. benstonei AB675710.1 121  TGCCCTCGACCGCCGGCCGAGCCCGCACCTTACTGCCTGCTCCAGGAGCGGCAACGGGGG

N. domei                181  TGCGGGGCAAGGCTTGGCACAAGAACGAACCCCGGCGCGGATTGCGCCAAGGAACGGTAA
N. benstonei AB675710.1 181  TGCCGGGCAAGGCTTGGCACAAGAACGAACCCCGGCGCGGATCGCGCCAAGGAACGGTAA

N. domei                241  CATAGCGTGCGCGGCCTCGCCGCCGGATGCCCGGCGAGCGAGGTGGCGACCTGTCGTATC
N. benstonei AB675710.1 241  CATAGCGTGCGCTGCCCTGCCGCCGGATGCCCCGCGAGCGAGGTGGCGACCCGTCGTATC

N. domei                301  TGAACGACTCTCGGCAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATG
N. benstonei AB675710.1 301  TGAACGACTCTCGGCAACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATG

N. domei                361  CGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTTGCG
N. benstonei AB675710.1 361  CGATACTTGGTGTGAATTGCAGAATCCCGTGAACCATCGAGTCTTTGAACGCAAGTGGCG

N. domei                421  CCCGAAGCCTCTAGGCTGAGGGCACGTCTGCCTGGGCGTCACGCATAGCGTCGCCCGCGA
N. benstonei AB675710.1 421  CCCGAAGCCTCTAGGCTGAGGGCACGTCTGCCTGGGCGTCACGCATAGCGTCGCCCGCGA

N. domei                481  CCAAGCCACCGCGTCTCTGCATGCTAGGTCGGGGCGGAGAGTGGCCTTCCGTGCGCCGTT
N. benstonei AB675710.1 481  CCAAGCCACCGTGTCTCTGCATGCTAGGTTGGGGCGGAGAGTGGCCTCCCGTGCGCCGTT

N. domei                541  GTGCGGCTGGCCTAAAATCGGAGCTCGGCGACTGCGCCAGGACTCCCGGTGGTCGACAAG
N. benstonei AB675710.1 541  GTGCGGCTGGCCTAAAATCGGAGCTCGGCGACTGCGCCACGACGTCCGGTGGTCGACAAG

N. domei                601  GCGAAGGCCA
N. benstonei AB675710.1 601  GCGAAGGCCA
```

Figure 13. Pairwise alignment (optimal Global alignment) of partial ITS sequences (610 bp) from *N. domei* sp. nov. and *N. benstonei* (AB675710.1) using BioEdit Sequence Alignment Editor. Unmatched nucleotides are not coloured and matching (conserved) nucleotides are represented by coloured blocks.

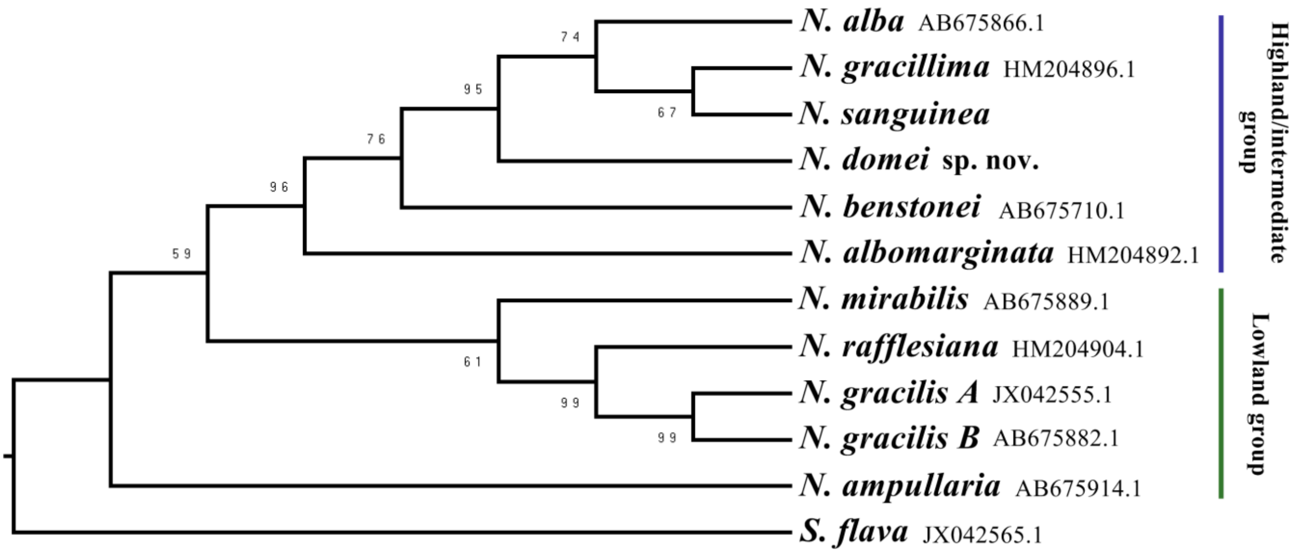


Figure 14. Phylogenetic tree (NJ method) reconstructed using ITS sequences obtained from the public database (NCBI) and ITS isolated in this study. Bootstrap values are as indicated above relevant branches and an American carnivorous pitcher plant (*Sarracenia flava*) serves as an outgroup.

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Studies on the Dipterocarpaceae of Borneo, II. Ant stipule-brood sites and extra floral nectary association in saplings of *Shorea macrophylla* [sect. Pachycarpae] in Sarawak, Malaysian Borneo

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Abstract. The presence of stipular and leaf blade extra floral nectaries and associated ant activity, including brood raising within stipules, is reported for saplings of *Shorea macrophylla* [sect. Pachycarpae] in Kuching Division, Sarawak.

Keywords: Dipterocarpaceae, *Shorea* Section Pachycarpae, *Rubroshorea*, Borneo, Sarawak, ants.

INTRODUCTION

The intricate and mutually beneficial associations existing between ants and tropical forest plants were first described for Asia by Beccari (1884–1886) and elaborated upon by Van Leeuwen (1913, 1923a,b,c). Subsequently an extensive body of literature has been generated for tropical Asia, notably for Euphorbiaceae (*Macaranga* – see for example Fiala et al. 1991), Rubiaceae (Huxley 1978; Razafimandimbison et al. 2005; Jebb & Huxley 2019), Melastomataceae (Clausing 1997), Apocynaceae (Kleijn and van Donkelaar 2001; Peeters & Wiwatwitaya 2014; Weissflog et al. 2017), and for the palm genus *Korthalsia* (Chan et al. 2012; Miler et al. 2016). Good general overviews for one lowland area of Peninsular Malaysia are provided of Fiala and Saw (2003) and Moog et al. 2003.

The Dipterocarpaceae, the dominant family of the canopy layer of lowland and hill forest in tropical Asia has no published reports of ant association on Borneo, despite the fact that the understory saplings of several species are routinely found with accompanying ants, especially at the active

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Figure 1. *Shorea macrophylla* Active shoot tip of sapling. Note the long revolute stipules and the pale elliptical extrafloral nectaries on the newest stipules.

Figure 2. *Shorea macrophylla* (A) active shoot tip of sapling. Note the long revolute stipules and the pale elliptical extrafloral nectaries on the newest stipules. (B) shoot tip of the red stipule expression. The extrafloral nectaries are clearly visible on the leaf blades. (C) detail of the amplexicaul bases of a stipule pair.

shoot tips. Here we report ant association and stipule nesting in *Shorea macrophylla* (de Vriese) P.S.Ashton [section Pachycarpae sensu Ashton 1963, 1982; *Rubroshorea* gen. nov. ined. sensu Maury 1978, 1979; Maury-Lechon 1979a,b, Maury-Lechon and Curtet 1998; see also Heckenhauer et al. 2017, 2018, 2019)]. To the best of our knowledge these are the first *in situ* observations for this species, although an image of extrafloral nectaries on the stipules of *S. macrophylla*, not native there but planted in the Forest Research Institute Malaysia, appears in Fiala and Saw (2003: Fig. 3).

Shorea macrophylla is a characteristic species of the forested flood plains a west Borneo, frequently developing almost pure stands and immediately recognizable by innovations with the long somewhat briefly persistent stipules (Figure 1 & 2). Saplings and young trees have disproportionately long wide-spreading plagiotropic branches typical of sect. Pacycarpae, with leaves of these branches distichously arranged and attached directly to the stem at the geniculum, in marked contrast to the spiralled leaves of the erect stem which have long slender petiole.

West Borneo has had four dipterocarp masting events over past five years with the result that it has been possible to study several large populations of saplings and young trees (up to 5m tall) of *Shorea macrophylla*. Observations revealed that almost every one of the several hundred plants we examined had *Crematogaster* ants associated with the active shoot tips, attracted to conspicuous extra floral nectaries on the exterior of the long stipules, and on the adaxial surface of the emerging and expanding leaf blades (Figure 3 & 4). Further examination of the typically revolute stipules revealed that they were often being used as brood chambers (Figure 5), with the loose edge of the tube packed with fragments of forest litter. On disturbance the ants hurriedly cleared the stipule of eggs (Figure 5). Although we did not see any active defence of the shoot tips by the ants

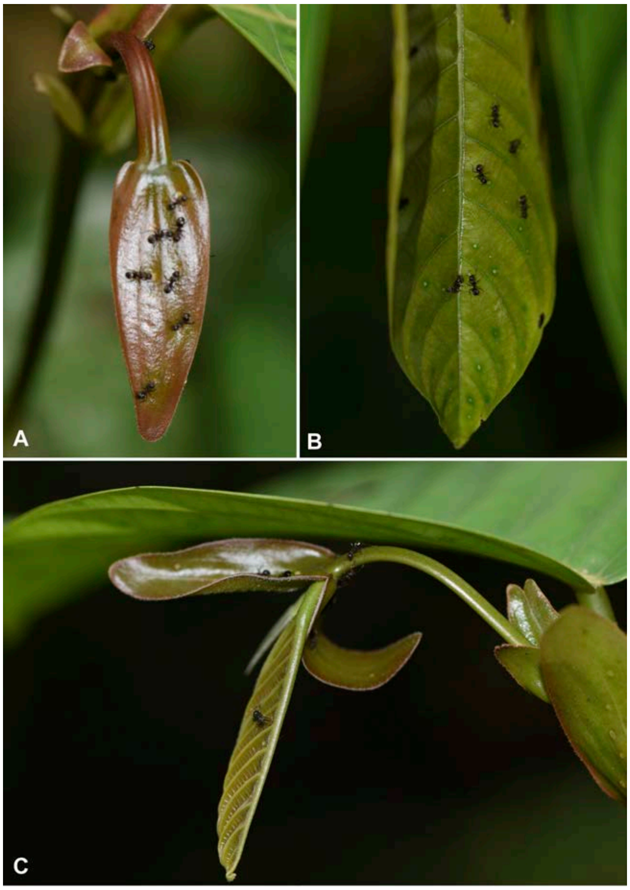

Figure 3. *Shorea macrophylla* (A) *Crematogaster* ants feeding on stipular extrafloral nectaries. (B) *Crematogaster* ants feeding on leaf blade extrafloral nectaries. (C) shoot tip with associated *Crematogaster* ants.

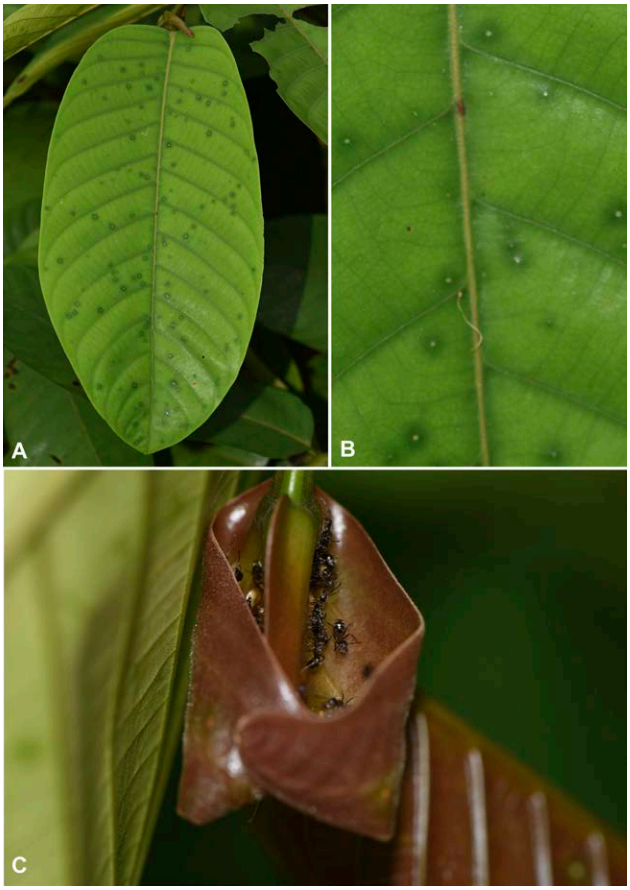

Figure 4. *Shorea macrophylla* (A) leaf blade showing extrafloral nectaries. (B) detail of leaf blade extrafloral nectaries. (C) shoot tip with associated *Crematogaster* ants.

against herbivorous pests, it was notable that none of the plants with ant association showed any sign of caterpillar and chrysomelid beetle damage to the leaf blades, whereas the few plants encountered without ants had extensive damage (Figure 6).

Although the observations presented here are solely associated with saplings and for a single species, and in no way a statistically proven set of data, they *are* compelling evidence that ant associations exist in Dipterocarpaceae and that both parties appear to gain advantage – food and brood sites for the ants and rather clear evidence that leaf blade damage is negligible in plants with associated ants. Much more detailed studies are required for *S. macrophylla* in particular to determine if ant associations continue into the mature tree canopy, and if they do whether the same of ants are involved, or if a different species is recruited, or if the exposure of the saplings results in different ant species associations. It is also important that the study is extended to more species of *Shorea* on Borneo. As it stands, we have evidence that two further species of sect. Pachycarpae (*Shorea splendida* (de Vriese) P.S.Ashton and a species we are yet to be able to name) have ant associations, although seemingly no nesting.

STIPULE CHARACTERS AND TAXONOMY

Given the ecological importance of the species, the local community level economic significance of the fruits ('nuts') as a source of a high grade fat (see for example Blicher-Mathiesen 1994), and by no means least that *Shorea macrophylla* is one of the most readily recognizable species of dipterocarp on Borneo, there is an remarkable level of taxonomic and morphological muddle and misinformation in the primary literature (Ashton 1982, 2004). In particular there is confusion concerning diagnostic characteristics, notably the erroneous report of flattened stipules (Ashton 2004: 204), and the supposed presence

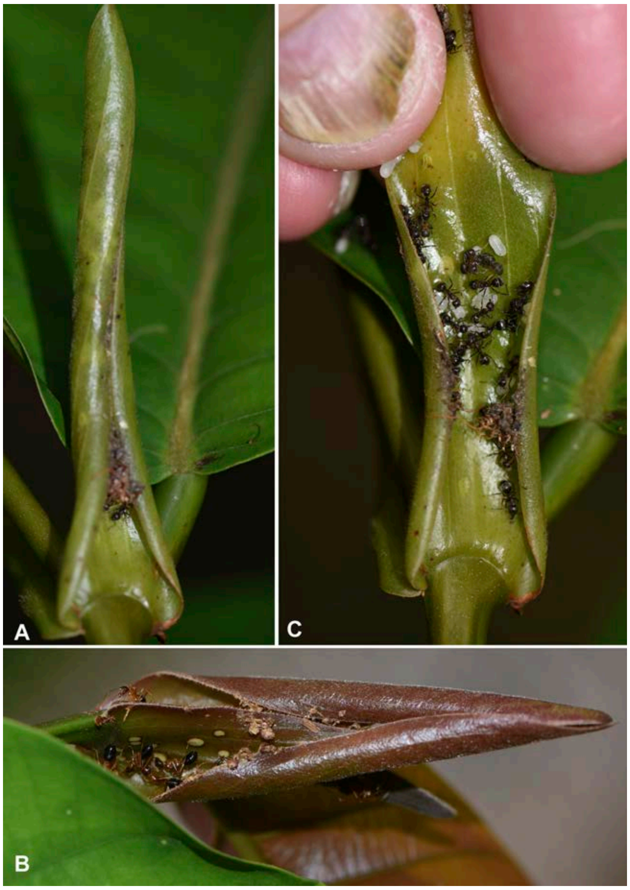

Figure 5. *Shorea macrophylla* (A) revolute stipule containing a *Crematogaster* ant brood chamber. Note the debris used to seal the open edges of the stipule. (B) the same stipule artificially opened with ants removing eggs. (C) another stipule brood chamber opened to show the (formerly external) extrafloral nectaries which are enclosed as the stipule margins recurves to fashion the tube.

of “persistently densely evenly pale brown pubesce(ense)” of “stipule…, petiole, leaf blade below, and midrib above”. In reality the stipules of *S. macrophylla* are consistently revolute (Figure 1, 2 & 5), while with the exception of the stipules, which are externally sub-microscopically glandular-stellate-pubescent, all the above-mentioned parts are entirely glabrous (Figure 5).

Remarkably, the conspicuous extra floral nectaries on the stipules and leaf blades (Figure 1 & 4) are not mentioned at all in the primary taxonomic literature, although Maury-Lechon & Curtet (1998: 11) state that “Extra-floral nectaries were recently found in many genera (Ashton, personal communication)”, the presence of such structures in African *Monotes* A.DC. was reported by Verdcourt (1989), and Balgooy et al. (2015), Fiala and Saw (2003), and Moog et al. (2003) all make note of their presence.

Figure 6. *Shorea macrophylla* (A) leaf blade showing typical chrysomelid beetle damage associated with saplings that have no ant association. (B) leaf blade showing typical caterpillar damage associated with saplings that have no ant association.

Given the above points, and that the sapling stages of most *Shorea* have never been adequately documented, and with that the descriptions of the often highly diagnostic stipules are often at best inadequate, it seems useful to provide a proper description here.

Shorea macrophylla (de Vriese) P.S.Ashton, Gard. Bull. Singapore 20(3): 278. 1963.

Stipules paired, tightly appressed in bud, soon divergent with the margins strongly revolute to fashion a tube, rather briefly persistent with the pair falling to leave a conspicuous scar by the time the associated shoot has increased in length by about five additional nodes; stipules equal, up to 5 cm long by 1.5 cm wide, rather narrowly lingulate, bases amplexicaul, briefly and narrowly auriculate, externally sub-microscopically glandular-pubescent, either dull rich red with scattered elliptical green extrafloral nectaries, or bright green with pale yellow nectaries, interior glabrous, somewhat waxy, concolorous with exterior, lacking extrafloral nectaries.

SCOPE FOR FURTHER WORK

Our observations are based on seedlings and saplings of a single species in detail, and two further species for which we have partial observations. Comprehensive studies of more species are highly desirable, especially in situations of high species diversity.

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A Review of North American *Isoetes engelmannii* (Isoetaceae) complex hybrids, including the description of *I.* × *fernaldii*, hyb. nov. and *I.* × *karenae*, hyb. nov.

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Abstract. The *Isoetes engelmannii* complex of eastern North America consists of 30 taxa including 13 named species. Nine of the 17 hybrids within the complex (the largest group of *Isoetes* hybrids in the world) have been formally described. Those named hybrids are reviewed here in light of recent additions to and enhancements of the morphological and cytological evidence employed in their original description. The pedigree of three of these, *I.* ×*brittonii*, *I.* ×*bruntonii* and *I.* ×*carltaylorii*, is updated and clarified. Formal descriptions are proposed for two additional taxa: ***I.* ×*fernaldii*, hyb. nov.** (*I. engelmannii* × *I. hyemalis*) and ***I.* ×*karenae*, hyb. nov.** (*I. appalachiana* × *engelmannii*). The potential for a further eight hybrid combinations to occur in the wild is also addressed.

Keywords: *Isoetes*, hybrids, *Isoetes appalachiana, Isoetes* × *brittonii*, *Isoetes* × *bruntonii*, *Isoetes* × *carltaylorii*.

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The diploid (2*n*=2x=22) *Isoetes engelmannii* A. Braun is an important species within the complex of larger, mostly polyploid aquatic/semi-aquatic quillworts (Isoetaceae) of eastern North America (Taylor et al. 1993; Taylor et al. 2017; Brunton & Troia 2018) (Figure 1).

Key to the development of our contemporary interpretation of this complex was the identification of the tetraploid (2*n*=4x=44) *Isoetes appalachiana* D.F. Brunton & D.M. Britton (Brunton and Britton 1997) within *I. engelmannii* sensu lato (s.l.) (Figure 2). With the identification of *I. appalachiana* as a distinct species, the potential number of hybrid combinations within this complex was virtually doubled. The two species are geographically centred on the Appalachian Mountains but are distributed (especially *I. engelmannii* sensu stricto [s.str.]) across much of the eastern United States. As per the discussion in the introduction (below) regarding the inclusive taxonomic concept employed here, the unnamed 'northern' and southern' genetic entities reported within *I. appalachiana* by Hoot et al. (2004) and others is acknowledged but not investigated further.

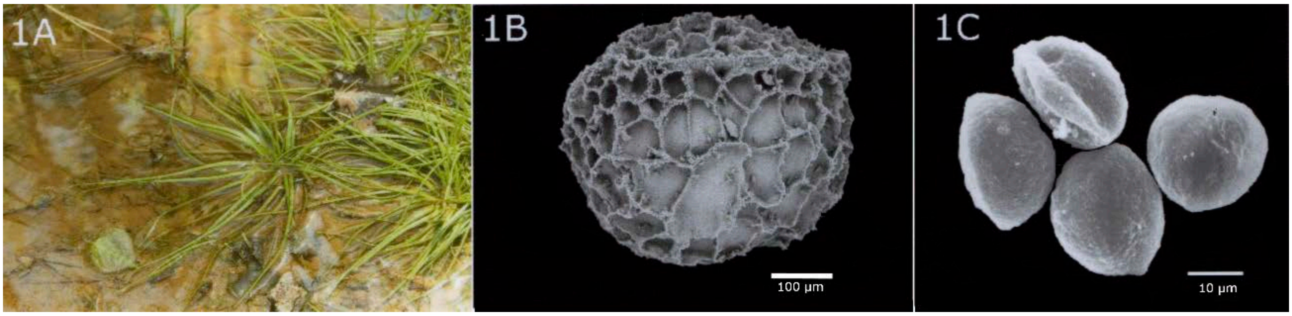

Figure 1. *Isoetes engelmannii* plant and spores. 1A: plants in shallow water of flowing stream, Stanley County, NC, USA, 3 April 2016 (Photo: D.F. Brunton); 1B: megaspore lateral view, 1C: cluster of microspores (*G. Engelmann s.n.*, September 1842, Jefferson County, MO, USA (Isotype - P).

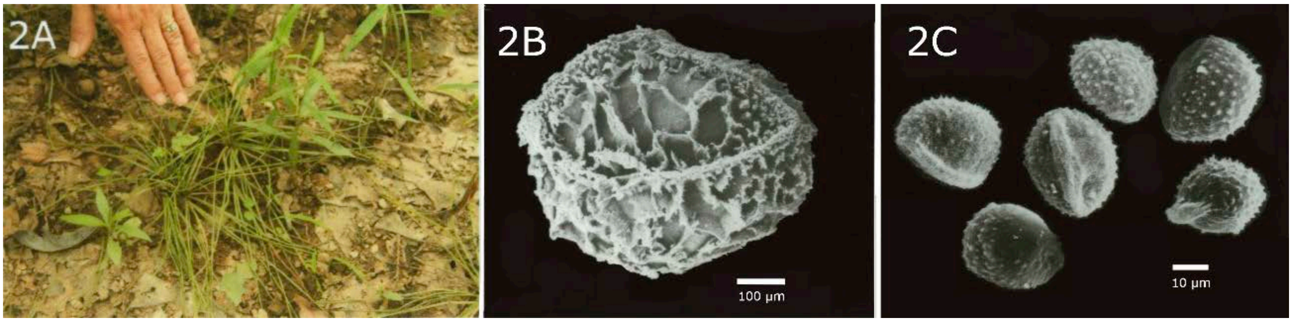

Figure 2. *Isoetes appalachiana* plant and spores. 2A: emergent plants in ephemeral woodland swale, Dinwiddie County, VA, USA, 20 June 2015 (Photo: D.F. Brunton); 2B: megaspore lateral view (*D.F. Brunton & K. L. McIntosh 11,171*, 6 July 1992, Huntington County, PA, USA (OAC), 2C: cluster of microspores (*D.F. Brunton & K. L. McIntosh 11,176*, 6 July 1992, Lycoming County, PA, USA (OAC).

The identification of sterile hybrids has been important in determining the distinctiveness of these and other *Isoetes* species by confirming the existence of interspecific genetic barriers (Taylor et al. 1985; Brunton 2015; Taylor et al. 2016). Indeed, hybrids are recognized as an important element of the evolution and taxonomy of vascular plants in general (Plume et al 2015; Gianguzzi et al. 2017; Goulet et al. 2017). Within the Isoetaceae, hybrids also commonly present opportunities for the development of polyploid species through alloploidy (Hickey et al. 1989; Troia et al. 2016; Brunton and Troia 2018).

The existence of hybrid diversity within the *Isoetes engelmannii* complex has been confirmed through recognition of a suite of often subtle but consistent and usually distinctive morphological features, often supported by cytology. Features and characteristics of the megaspores and microspores, found within sporangia at the base of fertile leaves, are critical to the identification of such plants. These include ornamentation patterns reflecting features of both putative parents.

Hybrids also have polymorphic, aborted megaspores and microspores, usually in high proportion, and a wide range of spore sizes within individual sporangia (Taylor et al. 1985; Hickey et al. 1987; Musselman et al. 1996; Britton and Brunton 1996; Troia & Greuter 2014; Brunton 2015). Megaspores of hybrids often present uniquely congested ('brain coral') ornamentation and/or are fused together as 'dumbbell-shaped' megaspores (Jeffrey 1937; Britton 1991; Taylor et al. 2016). Hybrid plants often display hybrid vigour and are larger than putative parents at the same site (Britton 1991; Musselman et al 1995). Cytology is an important determinant if the putative parents have different ploidy levels (Hickey et al. 1987; Taylor and Luebke 1988; Musselman et al. 1997).

Isoetes hybrids in the wild grow with at least one and almost always with both putative parents. They also are usually found in sites especially well suited to the mixing of spores, such as downstream of intrusions into river currents (e.g. below rapids) or in seasonally flooded creek-side swales (Britton and Brunton 1989; Britton and Brunton 1996; Musselman et al. 1996).

Isoetes species of environmentally stressed habitats often exhibit polymorphic spores reminiscent of sterile hybrids but still reflect only the ornamentation features of a single species. This is most commonly encountered in species of ephemeral wetlands such as temporary pools on bedrock outcrops (Haefner and Bray 2005; Brunton 2015). Environmentally induced spore polymorphism is rare in true aquatic species, however, and is almost always expressed in such plants by only a small number of individual spores. Dumbbell-shaped megaspores are apparently not evident in plants experiencing environmentally induced polymorphism (pers. obs.).

Recognition and clarification of many of the hybrid taxa in the *Isoetes engelmannii* complex occurred in a relatively short period of time in the 1990s - early 2000s. Subsequent cytological, taxonomic and morphological data have substantially altered initial conclusions for some of these taxa. Recent molecular studies (e.g. Shafran et al. 2018) indicate multiple origins in a number (most?) of the recognized polyploid *Isoetes* of eastern North America. This is perhaps to be expected within one of the most ancient and widespread vascular plant groups on Earth (Larsen and Rydin 2016; Wood et al. 2019). Especially so when many species within it, particularly amphibious and semi-terrestrial taxa such as some of those addressed here, consist substantially or entirely of widely dispersed populations in highly stressed environments, these habitat patches having persisted unchanged for thousands or in some cases, even millions of years (Pfeiffer 1922; McVaugh 1943; Matthews and Murdy 1969; Taylor et al. 1993; Heafner and Bray 2005; Brunton and Troia 2018).

Shafran (2019) states that "using a lineage-based species concept may require the recognition of ca. 50 new species of auto- and allopolyploid *Isoëtes* in eastern North America". There is a need for the systematic investigation of morphological, ecological and phytogeographic lines of evidence to provide consistent and repeatable collaboration with these molecular findings. This would demonstrate that genetic barriers exist between some of these newly distinguished 'species', and also would indicate how such taxa can be reliably distinguished in the field. In the absence of such collaboration, however, in the present study we hold to a conservative and inclusive (more traditional) taxonomic interpretation of *Isoetes* speciation. To do otherwise would preclude the identification of any sterile hybrids - indeed, the identification of many if not most populations of a particular polyploid *Isoetes* species – outside of the type location.

Clarifying the existence and status of sterile hybrids within already recognized *Isoetes* species will assist in future comprehensive, multifaceted investigations of relationships within the regionally important *Isoetes engelmannii* complex in particular and *Isoetes* in general.

METHODS

This study is based on extensive field experience of the first author undertaken since the early 1990s throughout the range all the species addressed. Over 2,250 voucher specimens of the taxa discussed here have been examined. The largest number of vouchers studied in over 30 herbaria are in CAN, DAO, DFB, FLAS, MICH, NYS, OAC and PH (herbarium acronyms of Theirs, continuously updated).

An extensive library of Scanning Electron Microscope (SEM) images prepared by D. M. Britton before 2007 (prepared with the methods described in Brunton and Britton 2006) of microspores and megaspores of virtually all subject taxa, was reviewed. Additional SEM images have been produced since 2017 by the authors. For these new images, air dried spores were attached to SEM stubs by means of adhesive carbon discs. These were sputter coated with a gold / palladium alloy (Au/Pd) and examined with a 2017 model FEI Apreo SEM (at 15 kV and 25 pA, with a working distance of 10 mm and a spot size of 6).

The physical characteristics of specimens, especially their megaspore form, ornamentation pattern and size, were examined through a Leica Wild M3B [light] dissecting microscope at 40x magnification, with the aid of an in-mount graticule (ocular micrometer) for measurements. Megaspore sizes reported for individual specimens represent the average width (across the equatorial region) of at least 10 spores. Comparable microspore measurements are based on the average of 20 longitudinal measurements taken from SEM images of clusters of spores.

Cytological determinations of hybrid specimens reported here were made by D. M. Britton, following the techniques described in Brunton and Britton (1999, 2006). Plants from sampled populations were grown in distilled water in a growth chamber. The developing root tips were excised and pre-treated in aqueous paradichlorobenzene (PDB) at room temperature for four hours. They then were washed in distilled water, fixed in acetic alcohol (3:1 absolute ethyl alcohol to glacial acetic acid) for 30 minutes or more, hydrolysed in Warmke's solution (1:1 concentrated HCl to absolute ethyl alcohol) for 7-10 minutes at room temperature, and stained in leucobasic fuchsin (Feulgen) for two hours. The meristems were squashed under a cover glass in 45% acetocarmine stain and examined.

RESULTS

Nine sterile hybrid combinations in the *Isoetes engelmannii* complex are reviewed (in alphabetical order) in light of ecological, distributional and taxonomic information developed since their original description.

Hybrid 1) *Isoetes appalachiana* × *I. engelmannii* (s.str.) (hyb. nov.)

Several individuals with classic sterile hybrid characteristics (as noted above), were found within a large mixed *Isoetes* population in Dinwiddie County, Virginia in 2015. Hundreds of *I. appalachiana* and scattered *I. engelmannii* plants were found in ephemeral swales and side channels along a permanent stream (Rowanty Creek) in seasonally flooded deciduous swamp forest (Figure 3). *Isoetes engelmannii* is common 100-200 m upstream along the creek as well (pers. obs.). Despite extensive collections in this area dating back to M. L. Fernald's investigations in the 1940s, no other *Isoetes* taxa have been found along Rowanty Creek within several kilometres of the site. *Isoetes hyemalis* D.F. Brunton occurs on an unnamed tributary of adjacent Stony Creek, however (see Hybrid 2, *Isoetes appalachiana* × *hyemalis*, below).

With both putative parents having predominantly reticulate megaspore ornamentation patterns, the range of distinctive features available for detecting this hybrid is reduced from that often available for the detection of other combinations. Nonetheless, there are several features of the Dinwiddie County material that confirm its distinctiveness.

The irregular shape, ornamentation and size of megaspores of Rowanty Creek hybrid plants are conspicuous (Figures 4A–4D). Megaspore size (514.9 µm, 1 SD 52.55 µm, N=28) was determined to be intermediate between that of diploid parent *I. engelmannii* (460-500 µm) and the tetraploid parent *I. appalachiana* (520-600 µm) (Brunton and Britton 1997; Brunton 2015). Most megaspores are distorted in shape (Figures 4A-4B), with some of the fused, dumb-bell shaped megaspores that are diagnostic of hybrids, also being evident (Figure 4B). Relatively few regularly globose megaspores that are typical of non-hybrid *Isoetes* plants were evident in the suspected hybrid plants.

Figure 3. Deciduous swamp forest habitat (in flood) of *Isoetes* ×*karenae* (*I. appalachiana* × *engelmannii*), Rowanty Creek, Dinwiddie County, VA, USA, 20 June 2015 (Photo: D.F. Brunton).

Microspore ornamentation is most similar to that of the smooth-spored diploid parent *Isoetes engelmannii* (Figures 4E-F), with only a subtle indication of the tuberculate ornamentation pattern of the tetraploid parent *I. appalachiana*. In keeping with this strong *I. engelmannii* expression in the hybrid, microspore size (25.4 µm, 1 SD 1.30 µm, N=40) was determined to be comparable to that diploid parent (25.5 µm) and substantially smaller than 30.4 µm length of tetraploid *I. appalachiana* microspores (Brunton and Britton 1997). A length of approximately 27-28 µm would have been more consistent with the size recorded with other triploid hybrids. This inconsistency, however, is believed to reflect the limited of microspore data (one plant) available at the Rowanty a mount Creek location.

At 17.6% (N=6, four plants as listed below), the average velum coverage of the sporangium of the hybrid is intermediate between putative parents *I. engelmannii* (10-15%) and *I. appalachiana* (20-25%) (Brunton and Britton 1997).

No fresh or live plants were available for genomic investigation or genomic analysis. That is unfortunate since the reflection of the different ploidy levels of the putative parents would have offered stronger support of the taxonomic hypothesis presented here. This necessitates the less desirable option of inferring ploidy level from spore size.

Other occurrences of this hybrid were detected in herbarium specimens showing comparable morphological characteristics (including aborted, polymorphic spores) from elsewhere in the sympatric range of the putative parents. In each case, the suspected hybrid was either a single huge plant (suggesting selective collection of individuals demonstrating such hybrid vigour) or mixed collections with one or both of the putative parents. The following binomial is proposed for this previously undescribed taxon:

Isoetes* ×*karenae D.F. Brunton and P.C. Sokoloff, **hyb. nov.**
(*Isoetes appalachiana* × *I. engelmannii*) (Figures 4A-4F).

Typus: United States, Virginia, Dinwiddie County: 40 m south along west bank of Rowanty Creek from Car-

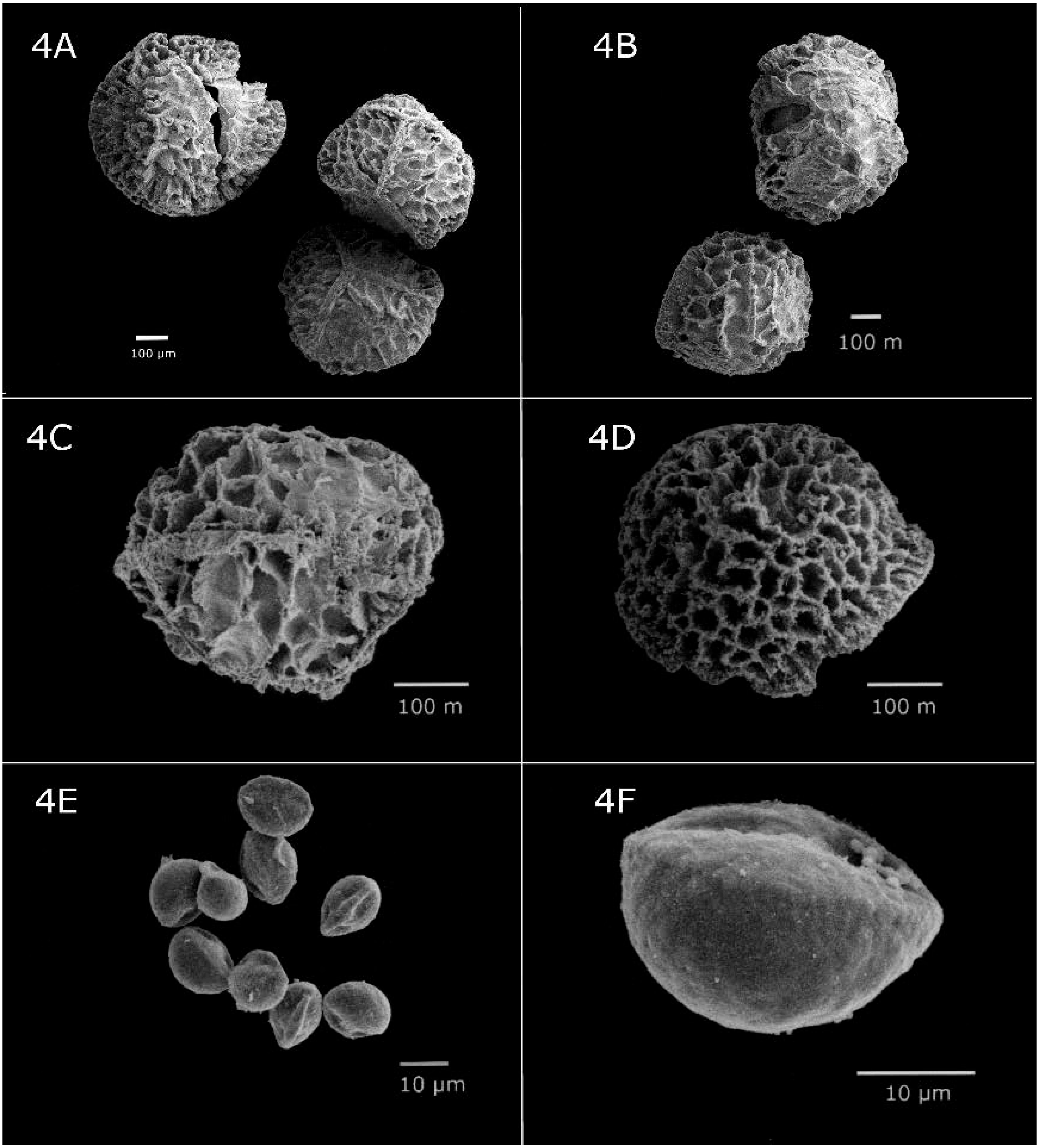

Figure 4. *Isoetes ×karenae* (*I. appalachiana* × *engelmannii*): 4A: cluster of polymorphic megaspores; 4B: misshaped and dumbbell-shaped megaspores; 4C: lateral view of megaspore; 4D: distal view megaspore; 4E: cluster of microspores; 4F: lateral view of microspore (*D.F. Brunton & K. L. McIntosh 19,008*, 20 June 2015, Dinwiddie County, VA, USA (CAN).

son Road (CR 703), 4.1 km west northwest of Carson, 20 June 2015, *D.F. Brunton & K. L. McIntosh 19,008* (holotype, CAN!)

Description

Plants – robust (more than 23 cm tall) in mixed populations with and gross form of putative parents *Isoetes* *appalachiana* and *I. engelmannii;* Megaspores – variable in size, most aborted (misshaped) with well-formed spores of intermediate size 514.9 µm (1 SD = 52.55 µm) in diameter and with densely, irregularly-reticulate ornamentation pattern formed by variable and ragged-crested muri; fused, dumb-bell shaped spores also present; Microspores – plain perispore surface obscurely verrucose, 25.4 µm (1 SD = 1.30 µm) in length; Habitat – in periodically flood-scoured bank swales along deciduous swamp forest creeks; Cytology – unconfirmed (inferred 2*n*=3x=33 from megaspore size).

Etymology

The taxon in named in honour of Canadian field botanist Karen L. McIntosh of Ottawa, Ontario, who not only discovered the type population but has provided valuable contributions to our understanding of numerous *Isoetes* taxa during 30+ years of field investigations with the first author across North America.

Paratypes

United States, Pennsylvania, Berks County: Birdsboro Reservoir, 1.8 miles southwest of Birdsboro [single, robust plant], 2 October 1932, *W.C. Brumbach 776-32* (PH); same site, 7 July 1934, *W.C. Brumbach 205-34* [large right-hand plant on mixed sheet with *I. engelmannii*] (PH); Lancaster County: York Furnace Road on Susquehanna River [very large (>33 cm tall) plant], 4 September 1924, *L. Sowden s. n.* (PH).

Isoetes ×karenae is very similar in appearance to *I. engelmannii ×hyemalis* (below), both being triploids involving the diploid *I. engelmannii* (s. str.) as one parent. *Isoetes ×karenae* megaspores, however, exhibit slightly thicker muri (Figures 4C, 4D vs. Figures 8C, 8D) and a more subdued equatorial ridge (Figures 4C vs Figure 8D). It also has microspores with obscurely verrucose surfaces (Figure 4F) rather than apparently obscurely broad-based spiny perispore of *I. engelmannii ×hyemalis* (Figure 8F).

Given the extent of overlapping distributions of its putative parents, *Isoetes ×karenae* can be expected to occur in mixed *Isoetes* populations over a large area in the eastern United States. Additional occurrences may be discovered at sites from central Pennsylvania southward to at least South Carolina and northern Georgia.

Hybrid 2) *Isoetes appalachiana × I. hyemalis* (*I. ×bruntonii* D. Knepper & L.J. Musselman)

This taxon was first described as a cytologically supported triploid hybrid, thought to represent *Isoetes engelmannii × I. hyemalis* (Musselman et al. 1996), prior to recognition that *I. engelmannii* (s.l.) included tetraploid *I. appalachiana* (Brunton and Britton 1997). *Isoetes ×karenae* (above) and *I. ×bruntonii* type locations are in adjacent creek systems in Dinwiddie County, Virginia. It is at a site well suited to the mixing of *Isoetes* spores and the generation of hybrids, where trees fallen into a woodland creek created back eddies where the spores of the locally abundant *I. hyemalis* could mix with those of other taxa (Figure 5). *Isoetes appalachiana* (e.g. *D. F. Brunton and K. L. McIntosh 12,557* (DFB, QFA), *14,519* (MIL), *16,097* (DFB, OAC, PH, MICH) and *19,011* (US) and *I. hyemalis* (e.g. *D. F. Brunton & K. L. McIntosh 12,221* (GA, MICH, MIL, VPI, DAO), *12,557* (CAN, DFB, TRT, BM), *13,118* (MIL. OAC), *16,096* (DFB, PH) and *19,010* (DFB, US) are the only species to have been found at the type location during repeated site investigations between 1995 and 2015 (pers. obs.).

Hybrid plants from the precise *Isoetes ×bruntonii* type location (L.J. Musselman and R. Bray, pers. comm.) were determined to be tetraploid (*D. F. Brunton, K. L. McIntosh, R. Bray & K. Haefner 13,559*, 17 May 1998 (OAC). The megaspores of multiple hybrid specimens obtained from that site between June 1995 and June 2015 (in DFB) also were found to have a coarser walled, more open ornamentation pattern (Figures 6A, 6B) indicative of *I. appalachiana* rather than *I. engelmannii* (s. str.). Hybrids involving *I. engelmannii* (s. str.) such as *I. ×altonharvillii* L.J. Musselman & R. Bray, *I. ×eatonii* R. Dodge, pro sp. sensu Taylor et al. (1985), and *I. ×foveolata* A.A. Eaton, pro sp. sensu Taylor et al. (1985) all exhibit more congested megaspore ornamentation. Megaspores from the holotype (ODU), an Isotype (DFB) and later cytologically determined tetraploid topotypes (*D.F.*

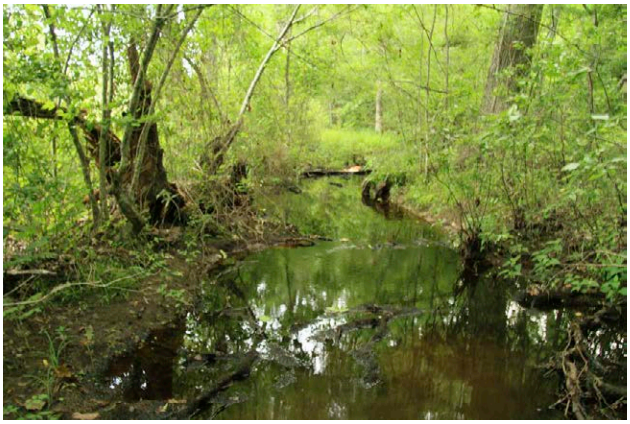

Figure 5. Woodland stream type location of *Isoetes ×bruntonii* (*I. appalachiana × hyemalis*), Dinwiddie County, VA, USA, 20 June 2015 (Photo: D.F. Brunton).

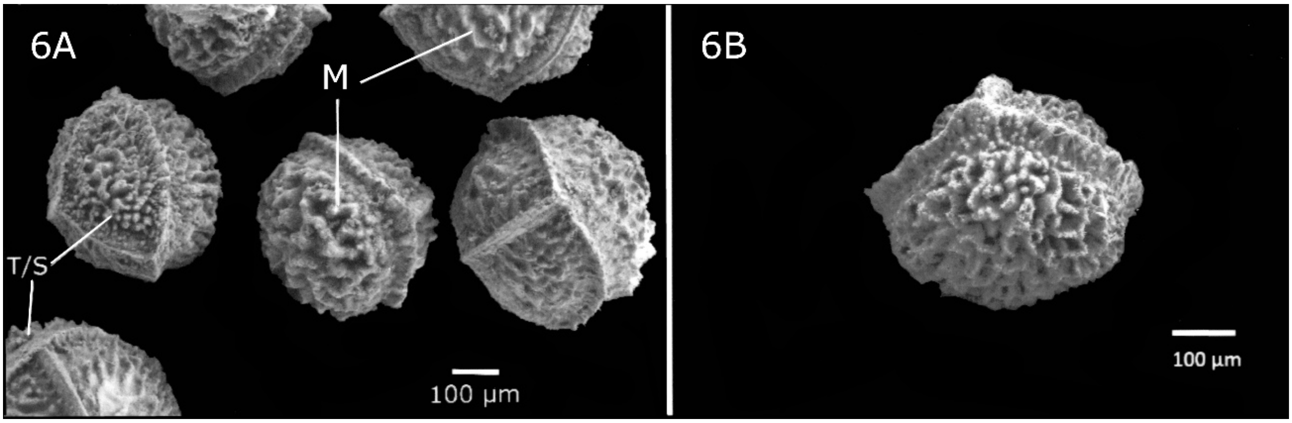

Figure 6. *Isoetes* ×*bruntonii* (*I. appalachiana* × *hyemalis*): 6A: cluster of polymorphic megaspores [T/S = tubercles or spines, M = interconnected muri]; 6B: lateral view of megaspore (*D.F. Brunton & K. L. McIntosh 19,011B*, 20 June 2015, Dinwiddie County, VA, USA (DFB).

Brunton & K. L. McIntosh 12,557B (1996) and *D.F. Brunton & K. L. McIntosh 19,011B* (2015) (DFB), range in size from 500 to 623 µm, averaging 517.4 µm (1 SD 33.24, N=80). This is a larger than the megaspores size found in triploid hybrids such as *I.* ×*karenae* (above) or *I. engelmannii* × *hyemalis* (below), which average approximately 500 µm. No microspores from type material were available for examination in the present study.

No diploid plants, nor any triploid plants since the original cytotype report (Musselman et al. 1996), have been reported at the *Isoetes* ×*bruntonii* type location. The isotype in DFB consists of two plants, one hybrid and one *I. appalachiana*. It is not possible to compare morphological data from the reported triploid cytotype against that of tetraploid hybrids later found at the type location as no voucher was retained of that cytotype (R. Bray, pers. comm.).

While it is technically possible that a triploid plant was originally present and has not reoccurred at the site, that 'one-off' occurrence would be contrary to our experience in all other regularly-producing hybrid sites. It seems most likely that either an error was made at the time of the original chromosome count for the cytotype or that the specimens did not originate from the *Isoetes* ×*bruntonii* type location. Regardless, existing cytological vouchers from the type location are exclusively tetraploid and morphologically consistent with the type material.

While *Isoetes* ×*bruntonii* is currently known only from eastern Virginia, it is reported (as *I.* ×*brittonii* D.F. Brunton & W.C. Taylor) to be frequent there (Musselman & Knepper 1994). Given the relative wide area of overlap between its putative parents, however, this hybrid could also be expected to occur in mixed *Isoetes* populations in North Carolina, South Carolina or even southern Georgia/ northern Florida.

Hybrid 3) *Isoetes appalachiana* × *I. septentrionalis* (*I.* × *brittonii*)

Brunton & Taylor (1990) described this hybrid before the existence of tetraploid *Isoetes appalachiana* was recognized within *I. engelmannii* (s.l.). As with *I.* ×*bruntonii* (above), that timing encouraged the assumption that a hybrid between a tetraploid (*I. septentrionalis – as I. riparia* G. Engelmann, pro parte [p.p.]) and *I. engelmannii* (s.l.), would be triploid. This misunderstanding was exacerbated by the selection of a cytotype not from the type location. That specimen (*W.C. Taylor 5,128B*, 9 Sept 1984, Middlesex County, Connecticut (MIL)) is recognized as probably representing *I. engelmannii* (s. str.) × *septentrionalis* (see Table 1).

The type location for *Isoetes* × *brittonii* in Lycoming County, Pennsylvania was selected because of the apparent abundance of hybrids at the site (pers. obs.). Its location at a bridge abutment intruding into the natural flow of the Susquehanna River presents ideal conditions for hybrid generation. Cytological determinations made after the Brunton and Taylor (1990) description of the taxon established that hybrid plants at the *I.* ×*brittonii* type location (e.g. *D. F. Brunton & K. L. McIntosh 11,176*, 6 July 1992 (OAC) were tetraploid 2*n*=4x=44 and that the associated *I. engelmannii* (s.l.) parent was tetraploid *I. appalachiana* (*D. F. Brunton & K. L. McIntosh 11,177*, 6 July 1992 (OAC), not diploid *I. engelmannii* (s. str.). Significantly as well, spore measurements from the holotype and cytologically confirmed topotypes (megaspores 542.8 µm (1 SD 55.93 µm, N=80), *W.F. Westerfold & H. A. Wahl 3,045*, 11 August 1951 (PH) and *D. F. Brunton & K. L. McIntosh 11,177* (DFB), and microspores 33.1 µm (1 SD 2.60 µm, N=11), *D. F. Brunton & K. L. McIntosh 11,177* (DFB), are more representative of tetraploids

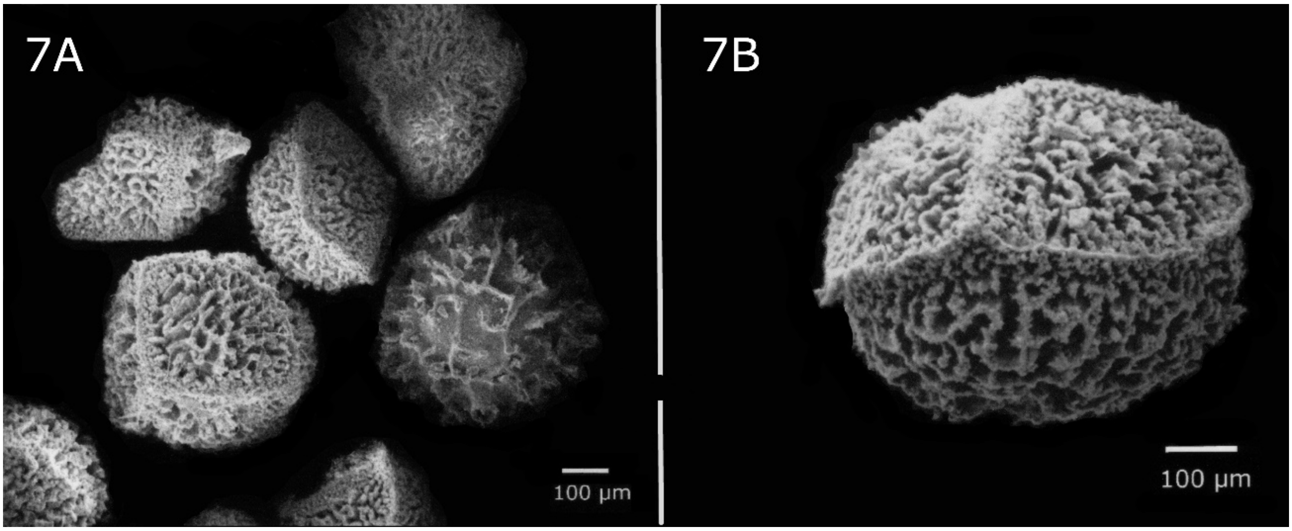

Figure 7. *Isoetes* × *brittonii* (*I. appalachiana* × *septentrionalis*): 7A: cluster of polymorphic megaspores (C.E. Waters s.n., 8 July 1904, Lancaster County, PA, USA, (MICH); 7B: lateral view of megaspore (*W.F. Westerfeld & H. A. Wahl 3,045*, 11 August 1951, Lycoming County, PA, USA (Isotype - PH).

than triploids, which average approximately 500 µm and 28 µm, respectively. The megaspore ornamentation of *Isoetes* ×*brittonii* also has a more open, less convoluted ornamentation pattern than would be expected were *I. engelmannii* (s.str.) actually the other putative parent with *I. septentrionalis* (Figures 7A, 7B).

Isoetes × *brittonii* remains a rare taxon, perhaps not surprisingly considering the relatively small area of overlap in the distribution of its putative parents (Brunton and Britton 1997; Brunton and McNeill 2015). It can reasonably be expected to occur elsewhere, however, in at least central and eastern Pennsylvania and adjacent New Jersey. It is presently known only in Pennsylvania from Lycoming County: West Branch Susquehanna River opposite Jersey Shore (*W. F. Westerfeld and H. A. Wahl 3045,* 11 August 1951 (Holotype - PAC); Union County: Lewisburg (*J. Montgomery s.n., 6 September 1962* (DFB)), and Lancaster County: McCall's Ferry, Susquehanna River (*C. E. Waters s.n.*, 8 July 1904 (MICH). It was apparently extirpated at the latter site by 20th Century dam construction.

Hybrid 4) *Isoetes engelmannii* (s.str.) × *I. echinospora* M. Durieu (*I. ×eatonii,* pro sp.)

The cytological criteria for hybridization in *Isoetes* were first described by Jeffrey (1937) who stated that *I. eatonii* [sic] was 'under strong suspicion of hybrid derivation'. This taxon was one of the first hybrid *Isoetes* taxa to be formally recognized (Taylor et al. 1985; Hickey et al. 1987). Diploid *I. ×eatonii* plants can be exceptionally large with leaves commonly over 30 cm long and some exceeding 60 cm in length (Dodge 1897). It is a true aquatic of freshwater ponds and streams, occasionally occurring in such large numbers as to hide the presence of one or both of its putative parents (Eaton 1900; Kott and Bobbette 1980). That abundance delayed recognition of its hybrid nature (Taylor et al. 1985). Its diploid hybrid status has been confirmed, however, by the morphological, ecological or cytological evidence coming forward in recent decades.

Isoetes ×eatonii occurs in the New England region of the United States and is disjunct to the west in southern Michigan (Palmer 2018) and southern Ontario, Canada (Britton et al. 1991). The population decline of parent *I. engelmannii* (s.str.) in this region (Taylor et al. 2016) has resulted in a comparable decline in hybrid occurrences as well.

Hybrid 5) *Isoetes engelmannii* (s.str.) × *I. hyemalis* (hyb. nov.)

This hybrid combination is known from a single site in eastern Virginia where it persisted, presumably through a series of independent propagation events, for over 30 years. A large (40 cm long), mature plant of at least several years of age was collected in 1965 and

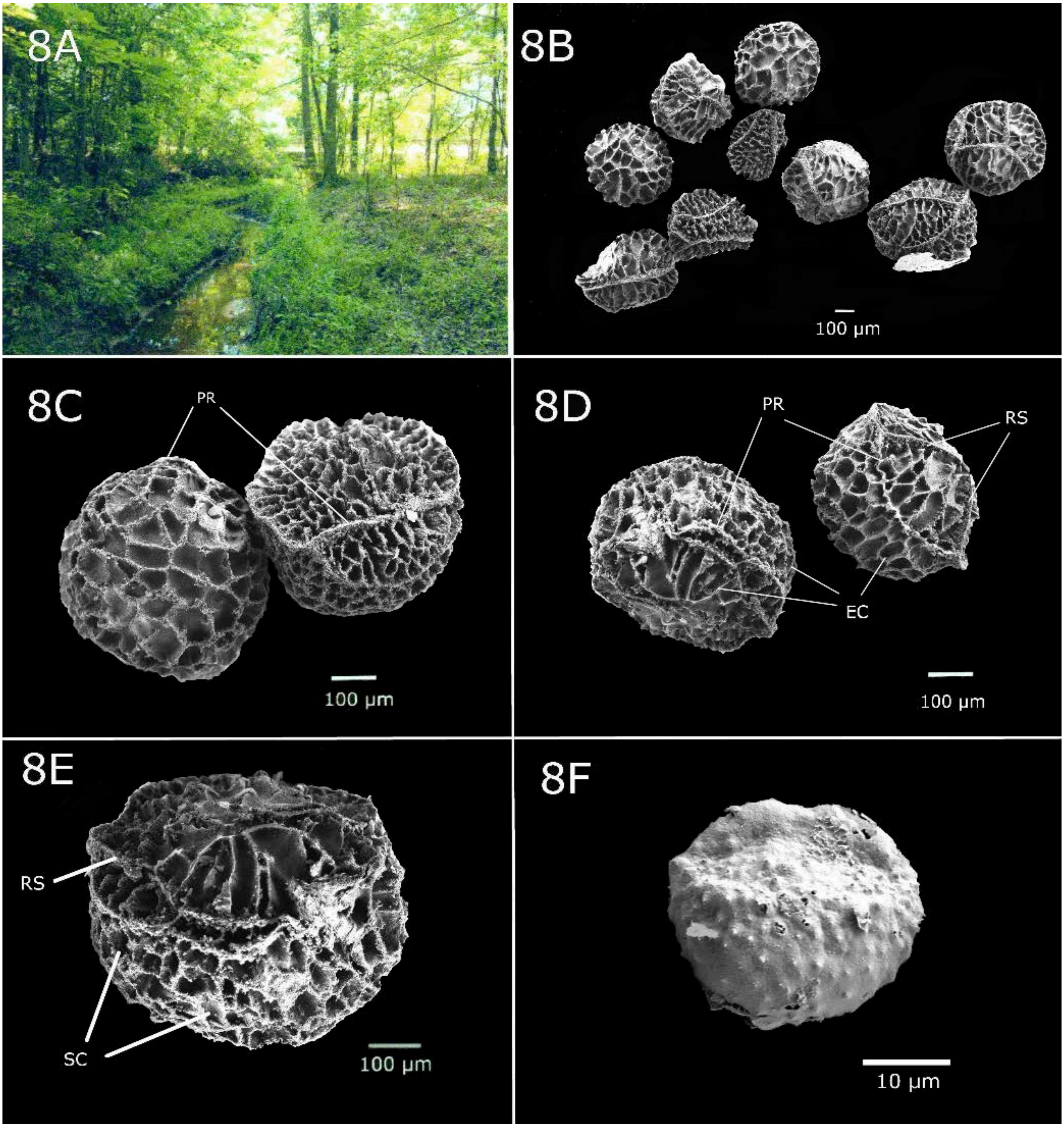

Figure 8. *Isoetes × fernaldii* (*I. engelmannii × hyemalis*): 8A: woodland stream habitat at type location (Gloucester County, VA, USA, 3 September 2016 (Photo: D.F. Brunton); 8B: cluster of polymorphic megaspores; 8C: distal and proximal view of megaspores with regularly reticulate cells [PR = pronounced suture ridges]; 8D: lateral view of megaspores with irregularly reticulate cells [EC = elongated cells, PR = pronounced suture ridges, RS = minute ridge spines]; 8E: lateral view of megaspore with densely reticulate ornamentation pattern [SC = small cells]; 8F: lateral view of weathered microspore (*D.F. Brunton & K. L. McIntosh 14,167*, 2 July 1999, Gloucester County, VA, USA (OAC).

smaller, cytologically confirmed hybrid plants were found at the same site in 1999. They were found in a small, permanently flowing creek along the edge of a deciduous woodland (Figure 8A) growing with numerous *I. engelmannii* and *I. hyemalis* plants. In August 2006, however, the site was severely impacted by flash

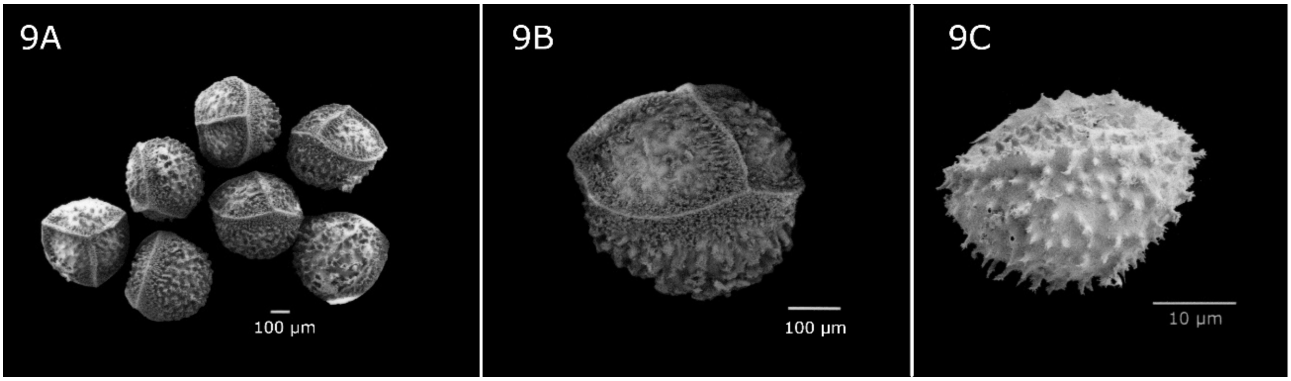

Figure 9. *Isoetes hyemalis*: 9A: group of regular-shaped megaspores; 9B: lateral view of megaspore; 9C: lateral view of microspore (*D.F. Brunton & K. L. McIntosh 11,165*, 4 July 1992, Harnet County, NC, USA (topotype - DFB).

flooding associated with Hurricane Ernesto and by subsequent ditch-clearing activity. *Isoetes* plants were not evident in September 2006 nor in a subsequent site visit in June 2015 (pers. obs.).

The leaves of the hybrid plants have the gross appearance of their putative parents and a velum coverage of their sporangium of approximately 17-20% (N=4). This is centred within the 10-25% range of velum coverage of the putative parents (Brunton et al. 1994; Brunton and Britton 1997). The hybrid also exhibits conspicuously polymorphic, aborted megaspores with congested, irregular ornamentation patterns (Figure 8B). The reticulate pattern of *Isoetes engelmannii* is the dominant expression on megaspores of these hybrid plants (Figure 8C), but appear to be of a less regularly 'honeycomb' pattern than is evident with that parent (Figure 1B). Megaspores of the hybrid also have a more congested, irregularly-reticular ornamentation on the distal side than is expressed in *I. engelmannii* and individual ornamentation 'cells' are conspicuously smaller (Figure 8C, 8E). The variation amongst megaspores of the hybrid includes some having more broken-reticulate pattern of muri (walls) interspersed with very short almost tuberculate muri on the proximal side (Figure 8C). Others exhibit an ornamentation pattern of elongated, non-reticulate cells (Figures 8D) more suggestive of tetraploid putative parent *I. hyemalis* (Figure 9A, 9B).

Well-formed megaspores of hybrid plants are intermediate in size (487.8 µm (1 SD 39.90 µm, N=30) between that of the diploid *I. engelmannii* (460 µm) and tetraploid *I. hyemalis* (522 µm) (Brunton et al. 1994 and Brunton and Britton 1997, respectively). Microspores from *Brunton & McIntosh 14,167* (OAC) are immature or weathered and their ornamentation pattern is somewhat obscured. Nonetheless, these microspores appear to have a sparse ornamentation of low, squat spines (Figure 8F) intermediate between that of smooth-spored *I. engelmannii* (Figure 1C) and conspicuously broad-spiny *I. hyemalis* (Figure 9C). Well-formed microspores are 27.9 µm (1 SD 1.59 µm, N=60) in size, which is intermediate between those of putative parents *I. engelmannii* (25.5 µm - Brunton & Britton 1997) and *I. hyemalis* (30.95 µm, 1 SD 1.76 µm, N=40), *Brunton and McIntosh 11,165*, Harnet County, North Carolina (OAC).

The following binomial is proposed for this undescribed taxon:

Isoetes* ×*fernaldii D.F. Brunton and P. C. Sokoloff, **hyb. nov.**
(*Isoetes engelmannii* × *hyemalis*) (Figures 8B-8F)

Typus: United States, Virginia; Gloucester County: southeast side of Piney Swamp Road (SR 635) at culvert for Piney Swamp, 2 km southwest of White Marsh, Gloucester County, 2 July 1999, *D.F. Brunton & K. L. McIntosh 14,167* (holotype, OAC! isotype (partial) DFB!).

Description

Plants - robust and exhibiting hybrid vigour (leaves to more than 40 cm tall), with gross form typical of putative parents *Isoetes engelmannii* and *hyemalis;* velum coverage of the sporangium 17-20%; Megaspores - variable in size, misshaped, frequently aborted; well-formed spores 487.8 µm (1 SD = 39.90 µm) in diameter with a congested, irregularly reticulate ornamentation pattern of irregularly tall muri; Microspores – sparsely ornamented with low, broad-based spines, 27.9 µm (1 SD = 1.59 µm) in length; Habitat - mixed populations growing with both putative parents in disturbed, periodically flood-scoured ditch along the edge of deciduous swamp forest; Cytology - 2*n*=3x=33 (*D.F. Brunton & K. L. McIntosh 14,167*, 2 July 1999 (OAC).

Etymology

The epithet acknowledges the contribution made by Merritt L. Fernald (1873-1950) to our knowledge of the distribution of this genus in the southeastern United States in general and Virginia in particular. His comprehensive field investigations in the 1930s and 1940s, especially on the species-rich coastal plain (Hugo and Ware 2012), laid the foundation upon which subsequent regional floristic and taxonomic investigations such as Pease (1951) and Musselman and Knepper (1994) are based.

Paratype

United States, Virginia, Gloucester County; dried up creek bed in Piney Swamp, 5 miles nw of Gloucester Point, June 12, 1965. *A.M. Harvill 12444* (GA!).

Isoetes ×fernaldii is similar in appearance to tetraploid *I. ×bruntonii*. Its smaller spore size, however, reflects its triploid status. It is even more similar in appearance to fellow triploid *I. ×karenae*. Compared with the latter, however, *I. ×fernaldii* exhibits megaspores with thinner, higher muri (Figures 8C, 8D vs. Figures 4C, 4D) and more pronounced suture ridges with a greater abundance of tiny spines along their flanks (Figures 8D vs. Figures 4C), and more evidently spiny microspores.

There is considerable overlap in the distributions of *Isoetes hyemalis* and *I. engelmannii* in the eastern United States. Accordingly, additional localities for this sterile hybrid are expected to be found, particularly in Virginia and the Carolinas.

Hybrid 6) *Isoetes engelmannii* (s.str.) × *I. macrospora* Durieu (*I. ×fairbrothersii* J. Montgomery & W.C. Taylor)

Isoetes ×fairbrothersii is the only hexaploid (2*n*=6x=66) taxon in the *I. engelmannii* complex. Its putative 10x parent *I. macrospora* (= *I. lacustris* L., sens. auct.) is a northern species that is disjunct as far south as New Jersey. It is distinctive from other *I. engelmannii* complex hybrids by its large (>530 µm) megaspores. Its megaspores also exhibit classic *Isoetes* hybrid characteristics, '*some* [being] *very large and spherical, others small and pyramidal, a few others dumbbell-shaped and some represented by wedge shaped fragments*' (Montgomery and Taylor 1994).

The hybrid is known only from a single freshwater lake in New Jersey where individuals were found infrequently in mixed populations with its putative parents, most frequently with *Isoetes macrospora*. With few areas of overlapping distribution by the putative parents, the possibility of additional populations of *I. ×fairbrothersii* being found are limited to northern New Jersey and adjacent eastern New York. Occurrences may also be possible, however, within the disjunct western populations of *I. engelmannii* in Michigan or Ontario (Cody and Britton 1989; Taylor et al. 1993, Tryon and Moran 1997; Palmer 2018; Weldy et al. 2019).

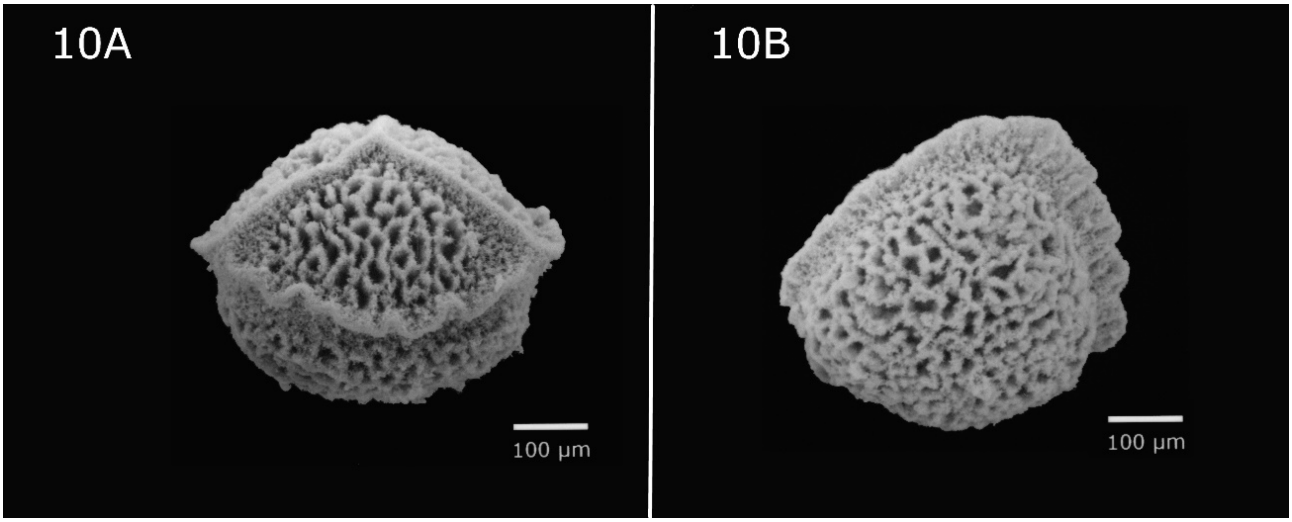

Figure 10. *Isoetes ×foveolata* (*I. engelmannii × tuckermanii*): 8A: lateral view of megaspore; 9B: distal view of megaspore (*A.A. Eaton 482a*, 20 August 1896, Rockingham County, NH, USA (Syntype - MICH).

Hybrid 7) *Isoetes engelmannii* (s.str.) × *I. riparia* G. Engelmann (s.str.) (*I. ×carltaylorii* L.J. Musselman)

Isoetes ×carltaylorii was originally described as the cytologically confirmed triploid hybrid between diploid *I. engelmannii* and tetraploid *I. acadiensis* L. Kott (Musselman et al. 1997). The latter is now considered to represent *I. tuckermanii* A. Braun ssp. *acadiensis* (L. Kott) D.F. Brunton (Brunton 2018)). The hybrid is known only from the tidal reaches of rivers flowing into the western side of the Chesapeake Bay in northeastern Virginia. It is unique amongst *I. engelmannii* complex hybrids in having a conspicuously subdued, reticulate megaspore ornamentation pattern of low, broad (almost vermiform) muri.

The tetraploid parent appears not to be *Isoetes tuckermanii* ssp. *acadiensis* but *I. riparia* var. *reticulata* (A.A. Eaton) G. Proctor, an uncommon (now rare?) endemic of emergent tidal shores in freshwater and brackish marsh habitat on the Chesapeake Bay (Proctor 1949). *Isoetes riparia* var. *reticulata* shares many morphological similarities with *I. tuckermanii* ssp. *acadiensis* (Brunton 2015), particularly in having a reticulate megaspore ornamentation pattern of low, broad (almost vermiform) muri. *Isoetes riparia* var. *reticulata* has consistently smaller megaspores with thinner, usually more densely arranged muri, however, and this intricacy is reflected in the megaspore ornamentation of the hybrid. In addition, *I. tuckermanii* ssp. *acadiensis* is a non-tidal freshwater species that extends no further south than Massachusetts, 650 km from the nearest *I. ×carltaylorii* site (Taylor et al. 1993; Musselman et al. 1997; Brunton 2018).

Isoetes ×carltaylorii is not likely to be found outside of the Chesapeake Bay of Virginia and the adjacent District of Columbia, the only area where the putative parents are sympatric.

Hybrid 8) *Isoetes engelmannii* (s.str.) × *I. tuckermanii* (*I. ×foveolata*, pro sp.)

Along with *Isoetes × eatonii*, this was thought to be a distinct species when described in the 19th Century (Eaton 1898) and is one of the first *Isoetes* taxa to be recognized as a hybrid (Taylor et al. 1985; Hickey et al. 1989). It is a true aquatic, found in ponds and rivers in southern New Hampshire and apparently has not been found in the wild for over a century. Megaspore ornamentation in this triploid is congested, presenting a particularly bold example of the 'brain-coral' pattern typical of *Isoetes* hybrids (Britton 1991) (Figures 10A, 10B).

Given the relatively large area of southern New England (Massachusetts, Connecticut, Rhode Island, New Hampshire) where its (at least formerly) common putative parents are sympatric, the rarity of this taxon is unexpected. This may reflect an ecological separation of the parents, *Isoetes tuckermanii* apparently occurring in more acidic substrates and oligotrophic water than *I. engelmannii* (pers. obs.).

Hybrid 9) *Isoetes engelmannii* (s.str.) × *I. valida* (G. Engelmann) W.N. Clute (*I. ×altonharvillii*)

This cytologically confirmed diploid typically exhibits the classic features of *Isoetes* hybrids including hybrid vigour, brain coral megaspore ornamentation patterns, fragmented and aborted spores and occurrence in ponds, seepages or along river shores with one or (usually) both of its putative parents (Musselman et al. 1995). The ca. 50% velum coverage of the sporangia reported for the hybrid is the same as that determined for *I. valida* (Brunton and Britton 1996). This is significantly greater than would be expected of a hybrid also involving *I. engelmannii* which has a much narrower (10-15%) velum coverage (Brunton and Britton 1996, 1997). Subsequently examined specimens of *I. ×altonharvillii* from Tennessee, North Carolina and South Carolina (DFB), however, average 26.6% velum coverage (N=28, six plants), which is consistent with expectations for an *I. engelmannii* × *valida* hybrid.

Isoetes ×altonharvillii has been found in mixed *Isoetes* populations in ponds and streams adjacent to and within the Appalachian Mountains from Delaware to northeastern Alabama, occasionally growing in relatively high elevation sites.

Potential Hybrid Combinations

In addition to the nine formally named hybrid taxa reviewed above, there are eight hybrid combinations which remain to be confirmed in the *Isoetes engelmannii* complex. Most of these involve species with restricted range and/ habitat requirements and thus have limited potential for interaction with other *Isoetes*. Putative parental taxa include *I. boomii* N.T. Luebke, *I. georgiana* N.T. Luebke, *I mattaponica* L.J. Musselman & W.C. Taylor and *I. microvela* D.F. Brunton. Table 1 lists and identifies the expected habitat, areas of occurrence (reflecting the sympatric range of the putative parents) and ploidy level of these presently unconfirmed hybrid combinations. The likelihood of discovery for each hybrid combination is subjectively appraised based on the apparent availability of suitable habitat and condi-

Table 1. Hypothesized *Isoetes engelmannii* complex hybrids.

Hybrid combinations	Ploidy	Probable habitat	Possible Area of Occurrence	Likelihood of Occurrence
Isoetes appalachiana × *I. boomii*	5x	ephemeral braided stream channels in deciduous swamp forest	Upper coastal plan, Georgia, northern Florida	Low
Isoetes appalachiana × *I. georgiana*	5x	ephemeral streams in deciduous swamp forest	Upper coastal plan, Georgia	Low
Isoetes appalachiana × *I. mattaponica*	3x	edges of freshwater tidal marshes or woodland freshwater stream outlets	tributaries of the Chesapeake Bay, Virginia	Low
Isoetes appalachiana × *I. microvela*	5x	Periodically flooded channels and stream bank swales within deciduous swamp forests	Coastal plain, North Carolina	Low
Isoetes appalachiana × *I. riparia* (s. str.) (coastal plain '×*brittonii*')	4x	ephemeral streams and emergent blackwater stream banks	Outer coastal plain, Virginia to northern North Carolina	Moderate
Isoetes appalachiana × *I. valida* (large-spored '×*altonharvillii*')	3x	Emergent, shaded streambanks and woodland seepage areas	Southern Pennsylvania to Alabama	High
Isoetes engelmannii × *mattaponica* (small-spored '×*carltaylorii*')	2x	Submerged along river shores adjacent freshwater tidal marshes	tributaries of the Chesapeake Bay, Virginia	Low
Isoetes engelmannii × *septentrionalis* (northern '×*bruntonii*')	3x	Shallow water and emergent shores of freshwater rivers and lakes	Southern New York, eastern Pennsylvania, Connecticut	High

tions for hybrid generation within the sympatric range of putative parents.

DISCUSSION

The complicated relationship within the diverse *Isoetes engelmannii* complex is depicted in Figure 11. Thirty taxa are represented, 13 of which are species, nine representing named sterile hybrids (including the two described here) and eight (listed in Table 1) being theoretically possible hybrids.

Specimens apparently representing some of the unconfirmed hybrid combinations noted in Table 1 are known. Herbarium specimens that appear to represent triploid *Isoetes engelmannii* × *septentrionalis* from Connecticut, New Jersey, Pennsylvania, New York and Maryland, for example, are deposited in MICH, MIL, PH and PSU. Most of these are fragmentary, pre-1950s specimens with limited site data, however. Confirmation of the natural occurrence of that and other possible hybrid combination requires stronger supporting evidence. Other vouchers suspected to represent unnamed *I. engelmannii* complex hybrids are old, fragmentary and/or ambiguous. They also are deemed insufficient to independently support formal designations.

In addition to enumerating the diversity and status of hybrids within the *Isoetes engelmannii* complex, the present study illustrates that the identification of such plants by morphological features alone is relatively straightforward. A suite of reliable morphological indicators of hybrid status has emerged from the investigation and description of over two dozen *Isoetes* hybrids in North America (Taylor et al. 1993; Musselman et al. 1994; Brunton and Britton 1999; Brunton 2015; Taylor et al. 2016), Japan (Takamiya 1999), eastern Russia (Mocholova et al. 2015), western Europe (Brunton et al. 2020) and India (Singh at al. 2018) over the last 25 years.

The determination of the parentage of hybrid plants in herbarium specimens on the basis of morphological features alone can be difficult. Indeed, without fully mature specimens and information on the associated *Isoetes* growing with a suspected hybrid, or in cases where voucher material is fragmentary or otherwise poorly preserved, identification may be impossible. This is particularly the case in differentiating hybrids between taxa of equal ploidy levels (and thus with spores of approximately the same size) and/ or with hybrid taxa sharing one putative parent, such as *I.* ×*karenae* and *I.* ×*fernaldii.* In these and most situations, the most compelling direct evidence of paternity can be the identity of the *Isoetes* species with which hybrid plants are growing.

Alloploidy involving the doubling of chromosome of interspecific hybrids is a common route of speciation in pteridophytes (Sigel et al. 2019) and is seen as an important (the most significant?) means for generating the current diversity of polyploid *Isoetes* species (Hoot 2004; Troia et al. 2016; Schafran et al. 2018). Accordingly, aligning important molecular indications of diversity with consistent phytogeographic, physiological, ecological and morphological lines of evidence is critical to the development of a coherent taxonomic understanding of

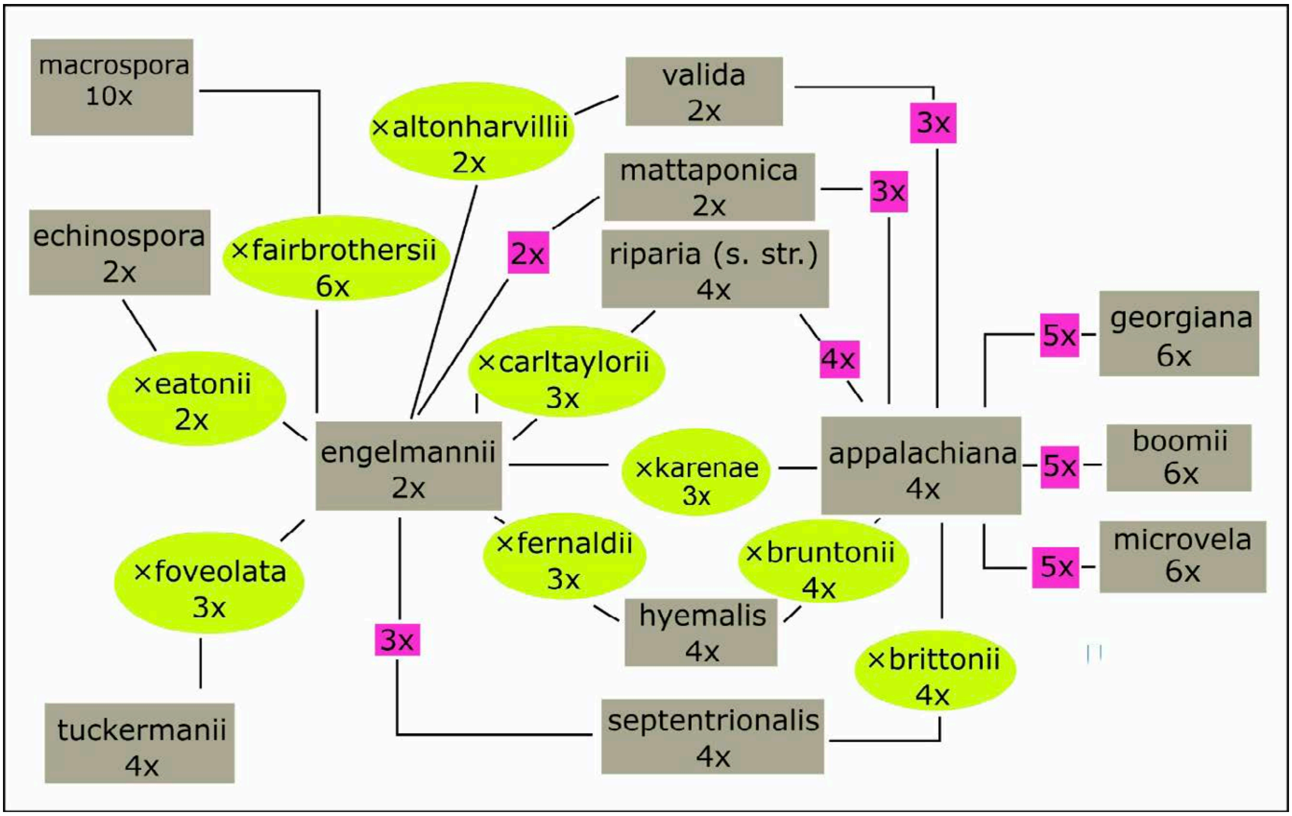

Figure 11. Relationships within the *Isoetes engelmannii* complex.

the genus. The present investigation contributes towards this by clarifying hybrid relationships within the important *I. engelmannii* complex. That process and these findings may also facilitate the identification of other sterile hybrids between populations within the dozens of undescribed, cryptic genetic entities recently reported from the eastern United States (Schafran 2019).

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Taxonomic significance of vegetative and reproductive morphology in southern Africa *Rhynchosia* sect. *Rhynchosia* (Fabaceae: Papilionoideae, Phaseoleae)

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Abstract. *Rhynchosia* is the largest genus in the subtribe Cajaninae, tribe Phaseoleae. Due to the lack of a recent taxonomic revision in the genus, the species are poorly known and as a result, are difficult to identify. As part of our ongoing taxonomic studies on the genus in southern Africa, this paper presents a comparative study of vegetative and floral morphological variation in the 47 species currently recognised in the type section *Rhynchosia* in the region. This is with a view to provide useful diagnostic morphological characters that can be used to correctly identify species in the type section and in other sections. The study used morphological data from field observation, herbarium specimens, and literature. Stems, leaves, and floral structures were examined with a dissecting microscope. A stereoscope with a *camera lucida* attachment was used to draw the reproductive morphology. Although morphological characters seem to overlap between the sections, characters such as leaflets size, type of indumentum on leaflet surfaces, stipules shape, type and length of inflorescences, presence or absence of indumentum on standard petals, presence and absence of sculpturing on wing petals, as well as length of upper lobes of the calyx are useful in identifying species.

Keywords: subtribe Cajaninae, tribe Phaseoleae, Leguminosae, Taxonomy.

INTRODUCTION

The significance of morphological characters in the taxonomy of the genera belonging to the family Fabaceae has been stressed by many researchers (Moteetee and Van Wyk 2006; Boatwright et al. 2010; Le Roux et al. 2010; Santos et al. 2012; Jeewon et al. 2013; Borges et al. 2018). Morphology has not only been useful in the identification and description of species within the family Fabaceae but has also been employed in phylogenetic studies and to understand the evolutionary patterns of plant taxa (LPWG 2017; Pinto et al. 2018; Silva et al. 2018). However, not all morphological characters are useful, while others are known to be more consistent, delimitative, or informative (Manoko 2007). For example, a superior ovary with one locule, two to many ovules arranged in two alternating rows on a single placenta, as well as marginal placentation are the most consistent characters that can be used to distinguish members of the family Fabaceae (Lewis et al. 2005).

The genus *Rhynchosia* Lour. belongs to the cosmopolitan family Fabaceae, tribe Phaseoleae, subtribe Cajaninae (Schrire 2005). It is the largest genus in its subtribe with a pantropical distribution and more than 230 species globally, ca. 55 in America, ca. 35 in Asia, ca. 69 in southern Africa, and ca. 64 in South Africa (Schrire 2005; Germishuizen 2006; Boatwright and Moteetee 2014; Ajao et al. 2018; Bezerra et al. 2019). Globally, it is found in America, Africa and Madagascar, Asia, and Australia. In Africa, its distribution ranges from West Africa (Ghana and Nigeria) to Tropical East Africa (Congo, Kenya, Tanzania, Uganda), Zambesiaca region (Botswana, Caprivi Strip, Malawi, Mozambique, Zambia, and Zimbabwe), and southern Africa (eSwatini, Lesotho, Namibia, and South Africa). In South Africa, it is found in all the nine provinces (Ajao et al. in preparation).

Previously, the South African species of the genus were revised by Baker (1923) whereby 59 species were recognized and placed in five sections, namely: *Rhynchosia* sect. *Arcyphyllum* (Elliott) Torr. & Gray., *R.* sect. *Chrysoscias* Benth., *R.* sect. *Cyanospermum* (Wight & Arnott) Benth., *R.* sect. *Polytropia* (Presl) Harv., and *R.* sect. *Rhynchosia*. However, *Rhynchosia* sect. *Arcyphyllum* is not represented in Africa as it is native to North America, hence the segregation of the *R. densiflora* (Roth) DC. group from the section to avoid phytogeographical confusion (Jaca and Moteetee 2018). Therefore, *R. densiflora* complex is currently recognized as a distinct group pending the outcome of the phylogeny of the genus *Rhynchosia*. Even though reproductive characters are regarded to be more important than vegetative characters, the latter can also be used to provide a distinction between species. Both characters have been used to delineate members of the family Fabaceae. For example, genera of subtribe Cajaninae, namely, *Adenodolichos* Harms, *Bolusafra* Kuntze, *Cajanus* DC., *Dunbaria* Wight & Arn., *Eriosema* (DC.) G.Don, *Flemingia* Roxb. ex W.T. Aiton, *Paracalyx* Ali, and *Rhynchosia,* are generally distinguishable from other members of the tribe by the presence of bulbous-based hairs, capitate trichomes, secretory-base trichomes and vesicular glands (Moteetee and Van Wyk, 2006; de Vargas et al. 2018; de Vargas et al. 2019). Furthermore, within the subtribe, the genus *Adenodolichos* is identified by the presence of bracteoles (absent in all other genera), while the structure of the fruits is of diagnostic importance in separating the genera *Cajanus* and *Dunbaria,* where they are transversely grooved in *Cajanus* but not in *Dunbaria*. Expanded and papery calyx lobes after flowering is diagnostic of the species in the genus *Paracalyx* while the genus *Flemingia* is identified by the sub-digitate or rarely unifoliolate leaves. The genus *Eriosema* is distinguished from *Rhynchosi*a by the following morphological characters: growth form or habit (subshrubs or erect, ascending, procumbent or prostrate, and never twining, vs. subshrubs or lianas/ erect, prostrate or twining), free or variably connate stipules (vs. always free stipules), absence of stipels (vs. stipels present in some species), hilum linear in shape (vs. hilum elliptical or oblong in shape), and funicle terminally attached to the hilum (vs. funicle centrally, subcentrally or occasionally terminally attached to the hilum) (Lackey 1981; Moteetee and Van Wyk, 2006; Cândido et al. 2019). A preliminary phylogenetic study in the genus by Manyelo (2014) revealed that the genus is not monophyletic as the other sections are embedded within the type section *Rhynchosia*.

In the ongoing taxonomic studies on the genus *Rhynchosia* in South Africa, reproductive and vegetative morphological characters have been successfully used to delineate species within groups, i.e. *R. densiflora* and *R. totta* groups and to revise *Rhynchosia* sect. *Chrysoscias*, *R.* sect. *Cyanospermum*, and *R.* sect. *Polytropia* (Moteetee et al. 2012; Moteetee et al. 2014; Moteetee and Le Roux 2016; Jaca and Moteetee 2018; Jaca et al. 2018). These morphological studies have also resulted in descriptions of a number of new species (Germishuizen 2011; Boatwright and Moteetee 2014; Moteetee et al. 2014; Ajao et al. 2018). The study here presented the morphological characters (reproductive and vegetative) of the species in the type section *Rhynchosia* in order to evaluate the characters that can be used to delineate species within the type section and between the other sections and group complexes.

MATERIALS AND METHODS

This study was based on the examination of herbarium specimens housed in BNRH, JRAU, and PRE (herbarium acronyms according to Thiers 2019) as well as on morphological observations of *Rhynchosia* species on the field. Stems, leaves, and floral structures were examined, and images were taken with a dissecting microscope with a digital camera attachment (OLYMPUS SZX2-TR30 JAPAN). Flowers were rehydrated in boiling water for 4–5 min, dissected under a binocular stereomicroscope and mounted in glycerol on a microscope slide for observation. A stereoscope with a *camera lucida* attachment was used to draw the reproductive morphology.

Data on both vegetative and reproductive morphology were taken from a minimum of five specimens per species in five replicates on each specimen except for some species with few available specimens. Also, a minimum of five mature flowers was dissected for each species with the exception of the species with few specimens available. Information regarding other sections and groups in the genus *Rhynchosia* was gathered from previously published studies from South Africa (Moteetee et al. 2012; Moteetee et al. 2014; Moteetee and Le Roux 2016; Jaca and Moteetee, 2018; Jaca et al. 2018). The taxon (*Rhynchosia* sect. *Rhynchosia*) studied is predominantly distributed in South Africa with some of the species extended to other southern African countries such as Botswana, eSwatini, Lesotho, Namibia, and Zimbabwe. The terminology used in this study is in accordance with the morphological species concept, as adopted by Grear (1978) and Isely (1990).

RESULTS AND DISCUSSION

A comparison of morphological characters between the species studied is presented in Table 1. Author citations are included here and will not be repeated elsewhere.

Vegetative Morphology

Growth habit

Rhynchosia species in the type section *Rhynchosia* are perennial herbs or shrubs with trailing, climbing, prostrate or erect to sub-erect or woody to sub-woody stems. Out of a total of 47 species that are currently recognized in the type section, 18 have erect or sub-erect growth form, these include *R. albissima, R. angulosa*, *R. bolusii, R. spectabilis, R. emarginata, R. pauciflora, R. sordia* and *R. sp. nov.* (Ajao et al. in preparation). The remaining species such as *R. caribaea, R. cilliata, R. fleckii, R. monophyla,* and *R. sublobata,* have trailing, climbing, or prostrate stems (Table 1, Figure 1). However, stems are woody at the base in some climbing or trailing species such as *R. capensis, R. coddii*, *R. fleckii, R. ovata* as well as taxa in the *R. totta* complex group (*R. totta* var. *totta*, *R. totta* var. *longicalyx*, *R. totta* var. *rigidula*, *R. totta* var. *venulosa* (Germishuizen 2011; Moteetee and Le Roux 2016). In sections *Cyanospermum, Chrysoscias* and *Polytropia,* stems are climbing, twining and trailing, whereas in the *R. densiflora* group they are twining, erect or prostrate (Moteetee et al. 2012; Moteetee et al. 2014; Jaca and Moteetee 2018; Jaca et al. 2018).

Indumentum

Stems are usually glabrescent to pubescent pilose to tomentose, velvety or villous with bulbous-based hairs and vesicular glands. Species such as *R. albissima*, *R. argentea*, *R. clivorum*, *R. crassifolia*. *R. emarginata*, *R. spectabilis*, and *R. waterberbergensis* have tomentose stems, in *R. woodi* and *R. angulosa* it is cano-pubescent or cano-pilose, while in *R. sordida* it is silky silvery-pilose and pilose in *R. ovata*. Taxa in the *R. totta* complex have stems that are usually glabrescent or pubescent with short hairs which are brownish or grey when young (Moteetee and Le Roux 2016). However, the stems are glandular in species such as *R. adenodes, R. arida, R. bullata, R. capensis,* and *R. cooperi* (Table 1). The indumentum type on the stems can be diagnostic as it can be used to distinguish between *R. caribaea* var. *caribaea* from *R. caribaea* var. *picta* in that it is pubescent in the former and tomentose in the latter.

Adaxial and abaxial surfaces of the leaves are usually glabrescent or pubescent to pilose or villous to velvety or tomentose, and glandular (yellow to orange or golden resin or dotted glands). Absence or presence of glands, and their distribution, can be of diagnostic importance in separating two morphologically similar species. For example, *R. nitens* shares tomentose stems and discolorous, silky silvery or velvety leaflets with *R. galpinii*. The former can be distinguished from the latter by the presence of glands on the surfaces, while they are absent in the latter. *Rhynchosia adenodes* can be easily confused with *R. cooperi* due to morphological similarities, i.e. having ovate-orbicular or subrhomboid leaflets, pubescent standard petals and axillary inflorescences with flowers arranged towards the apex. However, based on the distribution of glands, *R. adenodes* can be distinguished by its leaflets that are glandular on both surfaces while in *R. cooperi* they are glandular on abaxial surfaces only (Figure 2).

Leaf

Like most species in subtribe Cajaninae, the leaves of *Rhynchosia* sect. *Rhynchosia* are usually trifoliolate (Baker 1923), and rarely unifoliolate (e.g. *R. waterbergensis*) or having both types (*R. monophylla*, *R. nervosa*, and *R. totta* var. *totta*). In *Rhynchosia* sect. *Cyanospermum* and *R.* sect. *Chrysoscias,* the leaves are trifoliolate and never unifoliolate, whereas sect. *Polytropia* have trifoliolate to simply or pedately bipinnate, bi-tri-jugate, pauci-jugate, or supra-decompound leaves with *R. densiflora* group (*R. densiflora* subsp. *chrysadenia* var. *chrysadenia* (Taub.) Verdc. and *R. densiflora* subsp. *chrysadenia* var.

Table 1. Morphological comparison between taxa in *Rhynchosia* sect. *Rhynchosia*.

Species	Habit	Leaflets shape	Stem indumentum	Inflorescence type	Inflorescence length (mm)	Number of flowers	Standard petal	Wing	Fruits shape
R. adenodes Eckl. & Zey	Prostrate	Ovate-orbicular or subrhomboid,	Puberulous or sparsely pubescent and glandular	Axillary raceme	35–80(100)	2–7	Pubescent and glandular	Glandular, with sculpturing	Oblong
R. albissima Grand.	Erect sub-shrub	Obovate, rhomboid or elliptic,	Tomentose	Axillary raceme	60–130	10– 20 or more	Pubescent and glandular	Glandular, with sculpturing	Oblong-falcate
R. angulosa Schinz	Erect herb or shrublet	Elliptic	Cano-pilose or cano-pubescent	Axillary raceme	30–80(120)	4–10	Glabrous	Glabrous, without sculpturing	Oblong-elliptic
R. atropurpurea Germish	Twining or climbing	Deltoid or rhomboid	Pubescent or pilose and glandular	Axillary raceme	60–150	7–13	Glandular	Glandular, with sculpturing	Oblong-falcate
R. argentea (Thunb.) Harv.	Climbing or creeping	Ovate	Tomentose	Axillary umbel	30–40	4–6	Pubescent and glandular	Glabrous, without sculpturing	Falcate
R. arida Stirt.	Erect straggling	Elliptic to ovate	Puberulous or glabrescent and glandular	Axillary raceme	15–30	2–4	Glabrous	Glabrous, with slight or no sculpturing	Oblong-falcate
R. bolusii Boatwr. & Moteetee	Erect or sub-erect (non-twinning)	Narrowly oblong to oblong	Densely pilose to glabrescent and glandular	Axillary raceme	±15–40	1 or 2	Glabrous	Glabrous, without sculpturing	Broadly oblong
R. bullata Benth. ex Harv.	Erect	Oblong	Pubescent and glandular	Axillary raceme	25–40(60)	1–2	Glabrous	Glabrous, without sculpturing	Oblong
Rhynchosia harmsiana Schltr. ex Zahlbr. var. *burchellii* Burtt Davy	Twining	Rhomboid to deltoid or ovate-rhomboid	Villous, pubescent to pilose	Axillary raceme	20–65	4–10	Glabrous	Glabrous, with sculpturing	Oblong-falcate
R. calvescens Meikle	Twining	Deltoid or rhomboid	Sparsely pubescent	Axillary raceme	20–80(100)	3–8	Glabrous	Glabrous, without sculpturing	Falcate
R. candida (Welw. Ex Hiern)	Erect	Rhomboid or obovate-rhomboid	Canescent-tomentose and glandular	Axillary raceme	10–15	2–4	Pubescent and glandular	Glabrous, with sculpturing	Falcate
R. capensis (Burn. F.) Schinz	Climbing	Oblong to oblong-lanceolate, or ovate	Glandular	Axillary umbel	18–55(70)	2–6	Glabrous	Glabrous, with sculpturing	Oblong-elliptic
R. caribaea (Jacq.) DC. var. *caribaea*	Twining	Rhomboid to ovate-rhomboid or deltoid	Pubescent	Axillary raceme	35–110	8–22 or more	Glabrous	Glabrous, with sculpturing	Falcate
Rhynchosia caribaea var. *picta* (E. Mey.) Baker f.	Twining or climbing	Deltoid or rhomboid	Tomentose	Axillary raceme	60–80 (100)	8–12	Pubescent	Glabrous, with sculpturing	Fruit not seen
R. cilliata (Thunb.) Schinz	Prostrating	Elliptic to oblong	Villous	Axillary raceme	15–25	1–2	Glabrous	Glabrous, without sculpturing	Oblong

(Continued)

Species	Habit	Leaflets shape	Stem indumentum	Inflorescence type	Inflorescence length (mm)	Number of flowers	Standard petal	Wing	Fruits shape
R. clivorum S. Moore	Erect	Ovate-elliptic or ovate-lanceolate	Tomentose	Axillary raceme	60–100 (140)	5 –10 or more	Glabrous	Glabrous, with sculpturing	Oblong
R. codii Germish.	Trailing	Narrowly elliptic to broadly ovate	Densely pubescent	Axillary raceme	10–25	2–5	Glabrous	Glabrous, without sculpturing	Oblong falcate
R. cooperi (Harv. ex Baker f.) Burtt Davy.	Climbing and twinning	Ovate or suborbicular	Pubescent and glandular	Axillary raceme	80–170(200)	10–20	Pubescent and glandular	Glabrous, with sculpturing	Not seen
R. crassifolia Benth. ex Harv.	Trailing and procumbent	Elliptic-ovate	Tomentose	Axillary raceme	150–230(280)	10–22	Pubescent	Glabrous, without sculpturing	Fruits falcate
R. emarginata Germish.	Erect	Obcordate or broadly obovate	Tomentose and glandular	Axillary raceme	20–70	3–5	Glabrous	Glabrous, without sculpturing	Falcate
R. fleckii Schinz	Climbing, semi-erect	Ovate to obovate or elliptic to sub-rhomboid	Densely Pubescent to tomentose and glandular	Axillary raceme	10–25	2–4	Glabrous	Glabrous, without sculpturing	Oblong
R. galpinii Baker f.	Erect or sub-erect	Obovate to oblong-obovate or elliptic	Tomentose or velvety	Axillary umbel	15–40	2–4	Pubescent	Glabrous, with sculpturing	Oblong
R. grandifolia Steud.	Prostrate	Ovate to suborbicular	Pilose to tomentose	Axillary raceme	70–120	7–10	Glabrous	Glabrous, without sculpturing	Fruit not seen
R. harveyi Baker f.	Prostrate or climbing	Orbicular-rhomboid to deltoild	Velvety	Axillary raceme	10–20 (40)	2–4	Glabrous	Glabrous, without sculpturing	Oblong
R. hirsuta Eckl. & Zeyh.	Twining or trailing	Obovate-suborbicular	Pubescent	Axillary raceme	100–170 (190)	6–13	Pubescent	Glabrous, without sculpturing	Oblong-falcate
R. holosericea Schinz	Trailing	Orbicular to orbicular-ovate	Pubescent to pilose	Axillary raceme	40–170	3–10	Glabrous	Glabrous,without sculpturing	Oblong-falcate
R. komatiensis Harms	Erect	Ovate or ovate-orbicular	Tomentose	Axillary umbel	15–25(40)	1–2 or 4–10	Pubescent and glandular	Glabrous, without sculpturing	Oblong-falcate
R. minima (L.) DC. var. *minima* Meikle	Climbing	Rhomboid, ovate or suborbicular	Glabrous to velvety	Axillary raceme	20–180	Many flowered up to 24	Puberulous to pubescent and glandular	Glabrous, without sculpturing	Semi-falcate or falcate
R. minima (L.) DC. var. *glandularis* Mothogoane and Moteetee	Prostrate	Rhomboid-ovate or suborbicular	Glabrous to velvety	Axillary raceme	40–150	Many flowered	Puberulous to pubescent and glandular	Glandular, without sculpturing	Oblong
R. minima (L.) DC. var. *magniflora*. Mothogoane and Moteetee	Twining and prostrate	Rhomboid-ovate or suborbicular	Glabrous to velvety	Axillary raceme	30–150 (250)	Many flowered	Puberulous to pubescent and glandular	Glabrous, without sculpturing	Oblong-obovate

(Continued)

Species	Habit	Leaflets shape	Stem indumentum	Inflorescence type	Inflorescence length (mm)	Number of flowers	Standard petal	Wing	Fruits shape
R. minima (L.) DC. var. *memnonia* (Del.) Meikle	Prostrate	Rhomboid-ovate or suborbicular	Densely velvety	Axillary raceme	30–130	Many flowered	Puberulous to pubescent and glandular	Glabrous, without sculpturing	Oblong
R. minima (L.) DC. var. *prostrata* (Harv.) Meikle	Prostrate	Rhomboid-ovate or suborbicular	Glabrous to velvety	Axillary raceme	20–130	Many flowered	Puberulous to pubescent and glandular	Glandular, without sculpturing	Oblong
R. monophylla Schltr.	Trailing	Ovate or ovate-orbicular	Pubescent and sometimes glandular	Axillary raceme	15–25	1–3	Glabrous	Glabrous, with sculpturing	Elliptic
R. nervosa Benth. & Harv	Prostrate or twinning	Elliptic to elliptic-oblong or sub-rhomboid,	Pubescent or hispid-pubescent	Axillary raceme	62– 135(210)	3–10	Glabrous	Glabrous, with sculpturing	Oblong-falcate
R. nitens Benth.	Erect	Broadly ovate to cordate-ovate or ovate-elliptic or suborbicular	Silky slivery or velvety to tomentose.	Axillary umbel	15–40	2–3	Pubescent	Glabrous, with sculpturing	Oblong-falcate
R. ovata Wood & Evans.	Trailing, semi-erect	Ovate to ovate-elliptic or suborbicular	Pilose	Axillary raceme	35–60	2–4	Glabrous	Glabrous, with sculpturing	Oblong
R. pauciflora Bolus	Erect	Oblong to linear or oblong-linear	Tomentose and glandular	Axillary raceme	35–80	1	Glabrous	Glabrous, with sculpturing	Oblong
R. pedunculata le Roux & Moteetee	Prostrate	lanceolate-elliptic	Pubescent-glabrescent	Axillary raceme	(30) 45–125	(1)2–4	Glabrous	Glabrous, without sculpturing	Oblong-elliptic
R. pentheri Schltr. ex Zahlbr var. *pentheri*	Prostrate	Sub-orbicular or rhombeo-orbicular	Pubescent or puberulous and glandular	Axillary raceme	120–170(240)	8–10	Glabrous sometimes glandular	Glabrous, or sometimes glandular with sculpturing	Oblong-falcate
R. pentheri Schltr. ex Zahlbr. var. *hutchinsoniana* Burtt Davy	Prostrate	Sub-orbicular or rhombeo-orbicular	Pubescent and glandular	Axillary raceme	145–210(242)	8–20	Glabrous	Glabrous, with sculpturing	Oblong-falcate or falcate
R. reptabunda N.E.Br.	Climbing	Ovate suborbicular	Stems densely pubescent or pilose	Axillary raceme	70–100(130)	4–9	Glabrous	Glabrous, without sculpturing	Oblong-falcate
R. resinosa (Hochst. ex A.Rich.) Baker	Climbing	Deltoid or rhomboid	Puberulous and glandular	Axillary racemeor terminal	60–150	6–12	Pubescent and glandular	Glabrous, with sculpturing	Oblong
R. schlechteri Baker f.	Sub-erect	Ovate	Glandular and Pubescent	Axillary raceme	30–80 (100)	2–6	Glabrous	Glabrous, without sculpturing	Oblong
R. sordida (E. Mey.) Schinz	Erect	Elliptic to elliptic-oblong or oblanceolate	Silky silvery to pilose	Axillary raceme	5–15(30)	1–5	Glabrous	Glabrous, without sculpturing	Oblong

(Continued)

Species	Habit	Leaflets shape	Stem indumentum	Inflorescence type	Inflorescence length (mm)	Number of flowers	Standard petal	Wing	Fruits shape
R. spectabilis Schinz	Erect	Ovate or ovate-orbicular or orbicular	Canescent-tomentose	Axillary umbel	18–30	2–5	Pubescent and glandular	Glabrous, with sculpturing	Oblong
R. sublobata Schumach.) Meikle	Trailing, creeping or climbing	Deltoid or rhomboid	Pubescent or pilose	Axillary raceme	90–180 (260)	(10–17) or more	Pubescent	Glabrous, with sculpturing	Oblong-falcate and inflated
R. thormcroftii (Baker f.) Burtt Davy	Twinning, climbing or trailing	Deltoid or rhomboid-ovate	Stem pubescent or pilose and glandular	Axillary raceme	30–80 (100)	3–10	Glabrous	Glabrous, without sculpturing	Oblong
R. totta (Thunb.) DC. *var. totta*	Twining or climbing, semi-erect	Linear-lanceolate, lanceolate, elliptic or ovate,	Puberulous or Glabrescent	Axillary raceme	10–40	1–3	Glabrous	Glabrous, without sculpturing	Narrowly oblong
R. totta var. longicalyx Moteetee & le Roux	Twining or climbing, semi-erect	Ovate to lanceolate	Puberulous or glabrescent	Axillary raceme	18–55	2–5	Glabrous	Glabrous, without sculpturing	Narrowly oblong
R. totta var. rigidula (DC.) Moteetee & le Roux	Twining or climbing, semi-erect	Lanceolate to elliptic	Puberulous or glabrescent	Axillary raceme	13–16	1–3	Glabrous	Glabrous, without sculpturing	Narrowly oblong
*R. totta var. venulosa (*Hiern) Verdc.	Twining or climbing, semi-erect	Lanceolate	Puberulous or glabrescent	Axillary raceme	23–40	2–4	Glabrous	Glabrous, without sculpturing	Narrowly oblong
R. villosa (Meisn.) Druce	Prostrate	Ovate to cordate-ovate or suborbicular	Villous to tomentose	Axillary raceme	100–200(250)	12–24	Glabrous	Glabrous, with sculpturing	Oblong-falcate
R. vendae Stirt.	Climbing	Rhomboid	Puberulous or sparsely pubescent	Axillary raceme	110–160	8–14	Pubescent and sometimes glandular	Glabrous, with sculpturing	Oblong-falcate
R. waterbergensis Ajao, Boatwr. & Moteetee	Erect	Ovate or orbicular-ovate	Canescent-tomentose	Axillary raceme	25–60	4–8	Pubescent and glandular	Glabrous, with sculpturing	Fruit not seen
R. woodi Schinz *i*	Erect	Obovate or ovate	Cano-pubescent	Axillary raceme	30–60 (80)	5–10	Glabrous	Glabrous, with sculpturing	Oblong
R. sp. nov.	Erect	Linear-lanceolate to oblong-lanceolate	Pubescent and glandular	Axillary raceme	(25–)30–42	1	Glabrous	Glabrous, without sculpturing	Oblong to broadly-oblong

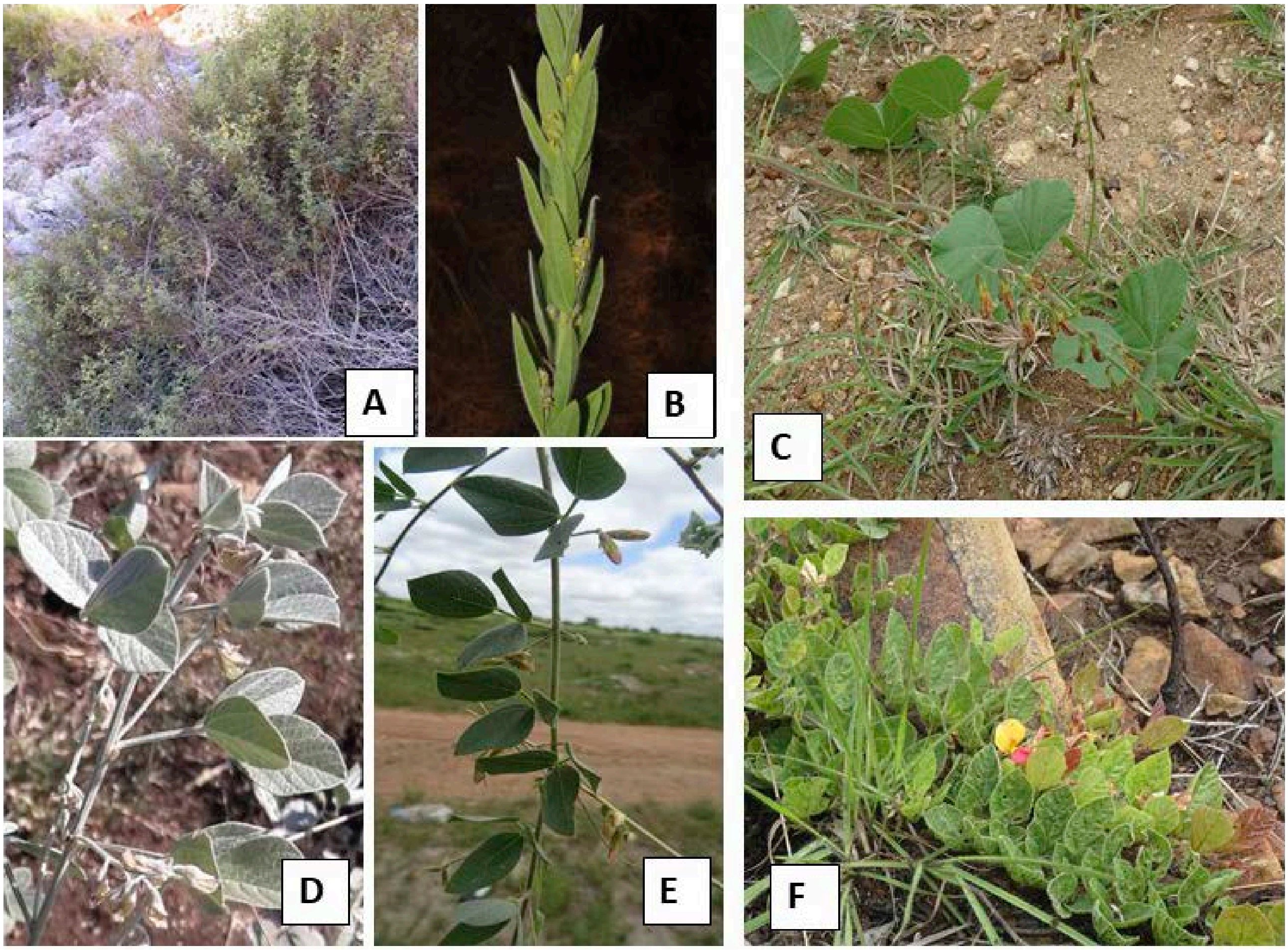

Figure 1. Growth habit of some *Rhynchosia* sect. *Rhynchosia* species. (A) Sub-erect stems of *R. schlechteri* (B). Erect stem of *R. sordida,* (C) Trailing stem of *R. sublobata.* (D) Erect stem of *R. albissima.* (E) Climbing stem of *R. fleckii.* (F) Trailing stem of *R. monophylla.* Photo by Pieter Mier (A), John Burrows (B), Mothogoane (D), Abdulwakeel Ajao (C,E,F).

connata (Baker f.) Jaca & Moteetee) having unifoliolate or trifoliolate leaves (Moteetee et al. 2012; Moteetee et al. 2014; Jaca and Moteetee 2018; Jaca et al. 2018). In this regard, the latter group is closely allied to the type section. In addition, the leaflet shape varies greatly in *R.* sect. *Rhynchosia* from oblong, linear to narrowly or broadly elliptic, ovate, obovate, obcordate, lanceolate, rhomboid and deltoid or sub-orbicular. The leaflets are linear to narrowly linear, or linear-lanceolate and lanceolate to oblong-lanceolate in *R.* sect. *Chrysoscias,* they are broadly elliptic to ovate or cordate in *R. sect. Cyanospermum* and lanceolate to linear-lanceolate, or elliptic to elliptic-lanceolate in *R.* sect. in *R.* sect. *Polytropia.* The presence of lanceolate to linear-lanceolate leaflets in both *R.* sect. *Polytropia* and *R.* sect. *Chrysoscias* suggests they are morphologically related. Furthermore, they are elliptic-ovate, rhomboidal to rhomboidal-ovate or almost round in *Rhynchosia densiflora* group. Leaf size can be as small 5–10 × 2–5 mm as in *R. bullata* and can be as big 45–150 (220) × 37–140 (230) mm in *R. villosa*. Leaf margins are usually entire but sometimes revolute in species such as *R. bullata, R. capensis, R. pauciflora,* and *R. sp. nov.* as well as species belonging to *R.* sect. *Chrysoscias* (Jaca et al. 2018). Leaf venation usually reticulate to cross-venulate, apices acute to mucronate or apiculate, acuminate or emarginate, bases rounded to oblique or cordate or cuneate.

Petiole and petiolule length is usually varied among the species, petioles are 1–63 mm long while petiolules are 2–30 mm long, and they are both usually pubescent to tomentose or pilose and glandular. Petiole length is of diagnostic importance in separating the different sections, for example, it is much longer in *R.* sect. *Cyanospermum* (up to 140 mm long), and much shorter in *R.* sect. *Chrysoscias,* (2.2–8.6 mm long), while *R.* sect. *Polytropia* and *R. densiflora* group range between the two

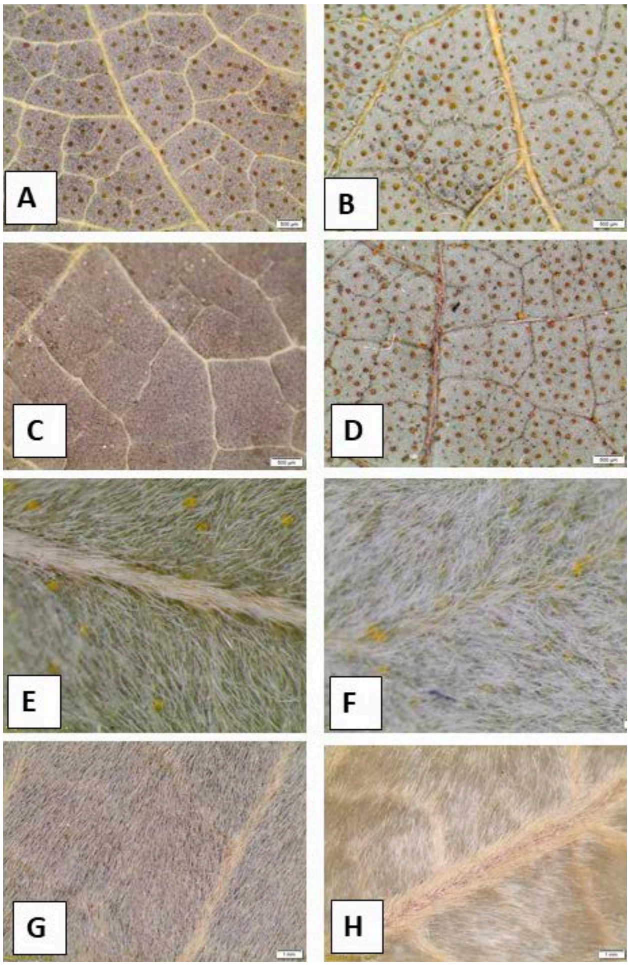

Figure 2. Variation in indumentum type and distribution on the leaflets of *Rhynchosia* sect. *Rhynchosia* species. (A,B) Adaxial and abaxial leaflet surfaces of *R. adenodes.* (C,D) Adaxial and abaxial leaflet surfaces of *R. cooperi.* (E,F) Adaxial and abaxial leaflet surfaces of *R. nitens.* (G,H) Adaxial and abaxial leaflet surfaces of *R. galpini.* Voucher specimens: (A,B) *Grobbelaar 1345* (PRE); (C,D) *Pienaar 557* (PRE); (E,F) *Bester 4429* (PRE); (G,H) *Pott 5315* (PRE).

(Moteetee et al. 2012, Moteetee et al. 2014; Jaca & Moteetee, 2018; Jaca et al., 2018). Within the sections, petiole length can sometimes be of diagnostic value, most especially in *R.* sect. *Rhynchosia* and *R.* sect. *Chrysoscias.* In *R.* sect. *Rhynchosia, R. nitens,* and *R. galpinii* are morphologically similar in having tomentose stems, discolorous, silky silvery or velvety leaflets, and pubescent standard petals. But the former can be distinguished from the latter in the longer petiole [(3)7–15(19) mm vs. 1–6 mm)]. In *R.* sect. *Chrysoscias, R. leucoscias* with much longer petioles (8–20 mm) can be distinguished from the other species in having shorter petioles, for example, *R. angustifolia* (2.2–4.5 mm), *R. chrysoscias* (3.5–7.8 mm), and *R. microscias* (3.0–) 4.3–8.6 mm) (Jaca et al. 2018).

Figure 3. Variation in stipules shape in *Rhynchosia* sect. *Rhynchosia* species. (A) Deltoid shaped stipule in *R. calvescens,* (B) Narrow lanceolate stipule in *R. caribaea* var. *caribaea.* (C) Large oblong-ovate with aristate or caudate apex in *R. clivorum.* (D) Long oblong-lanceolate or oblong-ovate in *R. reptabunda*. Voucher specimens: (A) *Acocks 20080* (PRE); (B) *Wells 4216* (PRE); (C) *Klein 197* (PRE); (D) *Ellan-Puttick 168* PRE).

Stipules are persistent, deciduous or caducous, pubescent or pilose to tomentose and glandular. They are quite varied in shape and can sometimes be useful in separating two morphologically similar species such as *R. calvescens* and *R. caribaea* which both have deltoid or rhomboid leaflets. However, the former can be identified by its deltoid stipules as opposed to lanceolate in the latter. *Rhynchosia clivorum* can also be identified by its large (7–13 × 4–6 mm), oblong-ovate stipules with aristate or caudate apex (Figure 3C). Stipule shape can also be used to some extent to distinguish different sections, for example in *R.* sect. *Cyanospermum* stipules are elliptic-lanceolate while in *R.* sect. *Polytropia*, they are ovate, but in *R.* sect. *Chrysoscias* the shape is quite variable. Within the latter section, *Rhynchosia leucoscias* and *R. angustifolia* are morphologically related in that they both have broad oblong stipules while *R. chrysoscias* and *R. microscias* have ovate-lanceolate stipules (Moteetee et al. 2012, Moteetee et al. 2014; Jaca et al. 2018). Stipels are usually absent in members of subtribe Cajaninae. However, there are few exceptions in some taxa of *Rhynchosia* sect. *Rhynchosia* (namely, *R. adenodes*, *R. cooperi*, and *R. pentheri* var. *pentheri*) where minute, caducous linear-lanceolate stipels occur. The presence of linear-lanceolate stipels was also reported in *R.* sect. *Cyanospermum* (Moteetee et al. 2012).

Reproductive Morphology

Inflorescence

In *Rhynchosia* sect. *Rhynchosia* flowers are usually arranged in axillary or terminal racemes or umbels (Wood and Key 2009). However, sometimes inflorescences are in axillary racemes but arranged towards the apex or summit as in *R. adenodes* and *R. cooperi (*Figure 4B). The inflorescence length ranges from 5 to 200 (280) mm, bears 1 to many flowers and can also be branched or unbranched**.** The inflorescence in *R.* sect. *Cyanospermum, R.* sect. *Polytropia,* and the *R. densiflora* group is an axillary raceme, while *R.* sect *Chrysoscias* has axillary umbels or solitary to sub-solitary flowers. On the other hand, the inflorescence is occasionally branched in *R.* sect. *Cyanospermum* (Moteetee et al. 2012; Moteetee et al. 2014; Jaca and Moteetee, 2018; Jaca et al. 2018). The branching pattern as well as the length of the inflorescences can sometimes be of diagnostic importance within *R.* sect. *Rhynchosia.* For example, *R. caribaea* var. *caribaea* and *R. caribaea* var. *picta* can be separated from other species in southern Africa with deltoid, rhomboid, or ovate-rhomboid leaflets such as *R. burchellii*, *R. atropurpurea, R. calvescens, R. sublobata,* and *R. thorncroftii*, by their branched inflorescences.

The peduncle is usually glabrescent to pubescent or pilose to tomentose in the genus (Ajao et al. in preparation). Regarding the usefulness of inflorescence length in species delimitation, *R. sordida* is a species that is similar to *R. angulosa* in that the leaflets are elliptic. *Rhynchosia sordida* can be distinguished from the latter by the inflorescence that is usually shorter than the leaflets (5–15(30) mm) versus inflorescence that is longer than the leaflets (30–80(120) mm) in *R. angulosa*. Therefore, species in the type section of *Rhynchosia* can be grouped into two groups based on the length of inflorescences. Species such as *R. cilliata*, *R. nitens, R. sordida, R. spectabilis*, and *R. komatiensis* etc. have inflorescences that are shorter than the leaflets while species such as *R. angulosa, R. atropurpurea, R. caribaea, R. clivorum, R. holosericea,* and *R. sublobat*a have inflorescences that are longer than the leaflets (Figure 4).

Flowers are usually pedicellate and yellow in all the species in the genus. To some extent, the number of flowers per inflorescence could be used to separate identical species in the genus. In the type section, for example, *R. ovata* is morphologically similar to *R. reptabunda* in that the stems are pilose, the leaflets are ovate or suborbicular and the bracts are persistent. However, *R. ovata* can be distinguished by its shorter inflorescence (35–60 mm long) with fewer flowers (2–4-flowered), whereas in *R. reptabunda* the inflorescence is 70–100(130) mm long and 4–9-flowered. Another example is found between *R. bolusii* and *R. capensis* which are similar in leaflet shape, but the former can be identified by its 1- or 2-flowered inflorescences vs. 1–6-flowered in the latter (Boatwright and Moteetee 2014). In *Rhynchosia* sect. *Polytropia*, *R. ferulaefolia* is similar to *R. pinnata* in having a non-twining habit and clustered inflorescences, but they can be distinguished based on the number of flowers, i.e. 5–12 in the former and 5–8 in the latter (Moteetee *et al.* 2014).

Bracts and bracteoles

In *Rhynchosia* sect. *Rhynchosia* bracts are usually lanceolate to ovate, deciduous or caducous to persistent, 1–6 × 0.2–3.0 mm, pilose or pubescent and glandular; bracteoles are absent. The absence of bracteoles is one of the diagnostic characters that separate the genus *Rhynchosia* and other genera in the subtribe Cajaninae (namely, *Bolusafra*, *Cajanus, Dunbaria*, *Eriosema*, *Flemingia*, and *Paracalyx*) from the genus *Adenodolichos* (Moteetee and Van Wyk 2006).

Flower structure

The calyx is generally bilabiate in all the species in the genus, with unequal lips and lanceolate to acuminate, broadly lanceolate or obtuse lobes. The calyx tube is 1–6 mm long, the upper lobes are usually the shortest and are always connate almost to the apex, sometimes halfway and rarely below halfway, 0.3–13 mm long, the lateral lobes are 1.5–18 mm long while the carinal lobe is usually longer than the other lobes (2–21 mm long). The length of lobes, as well as the extent of connation of the upper calyx lobes, can be of diagnostic value within the type section and the *R. densiflora* group. A noteworthy example in the type section is found between *R. sordida* and *R. angulosa* which share elliptic leaflets as well as an erect habit. However, *R. sordida* can be distinguished by its much longer upper calyx lobes (6–10 mm) when compared to those of *R. angulosa* (1–3 mm) (Figure 5). In the *R. densiflora* group, the upper lobes of the calyx are connate less than halfway to almost entirely, these character states are useful to separate the species in the complex. In *R. densiflora*

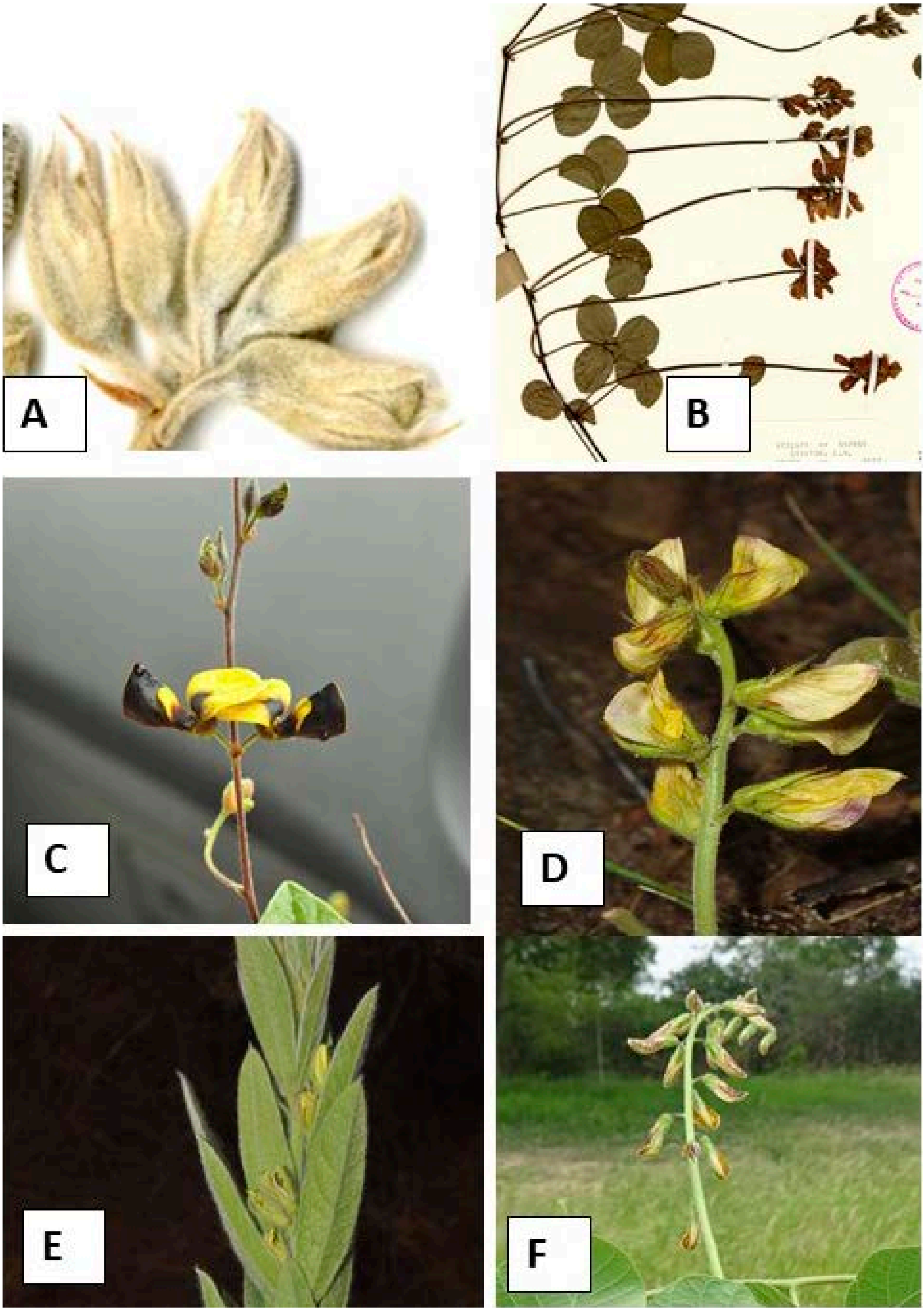

Figure 4. Variation in inflorescence type and length in *Rhynchosia* sect. *Rhynchosia* species. (A) Umbel inflorescence shorter than the leaflets in *R. spectabilis.* (B) Axillary inflorescence arranged towards the apex in *R. cooperi.* (C) Axillary inflorescence with flowers with purplish keel petals in *R. atropurpurea.*(D) Axillary inflorescence longer than the leaflets in *R. angulosa.* (D) Inflorescences shorter than the leaflets in *R. sordida.* (F) Axillary inflorescence in *R. sublobata.* Voucher specimens: (A) *Bester 11418* (JRAU); (B) *Stirton 8107* (PRE). Photo by John Burrows (C,D,E), Abdulwakeel Ajao (F).

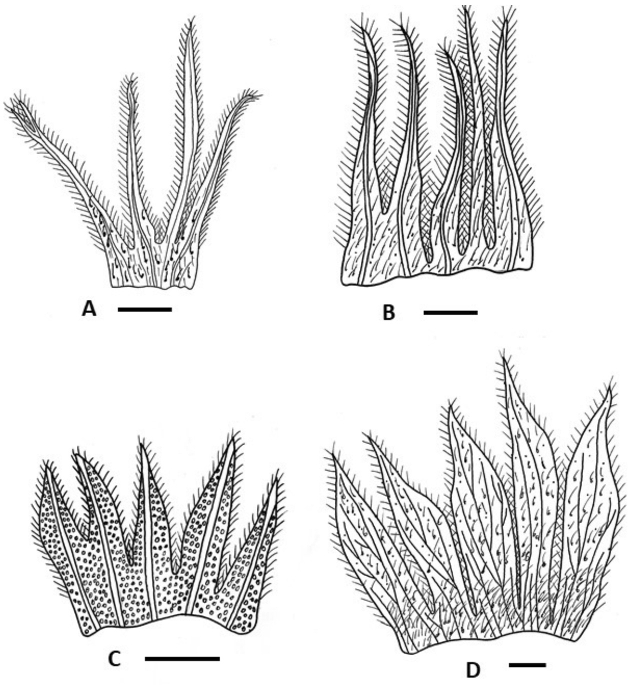

Figure 5. Variation in length of the calyx lobes in *Rhynchosia* sect. *Rhynchosia* species. (A) Upper lobes of the calyx connate to the apex in *R. angulosa*. (B) Upper lobes of the calyx connate to the base in *R. sordida*. (C) Upper lobes of the calyx connate to the apex or halfway in *R. capensis*. (D) Upper lobes of the calyx connate to the base in *R. clivorum*. Voucher specimens: (A) *Rogers 21907* (PRE); (B) *Mngomezulu 9* (PRE); (C) *Vlok 708* (PRE); (D) Galpin 14290 (PRE). Scale bar 1 mm. Drawn by Abdulwakeel Ajao.

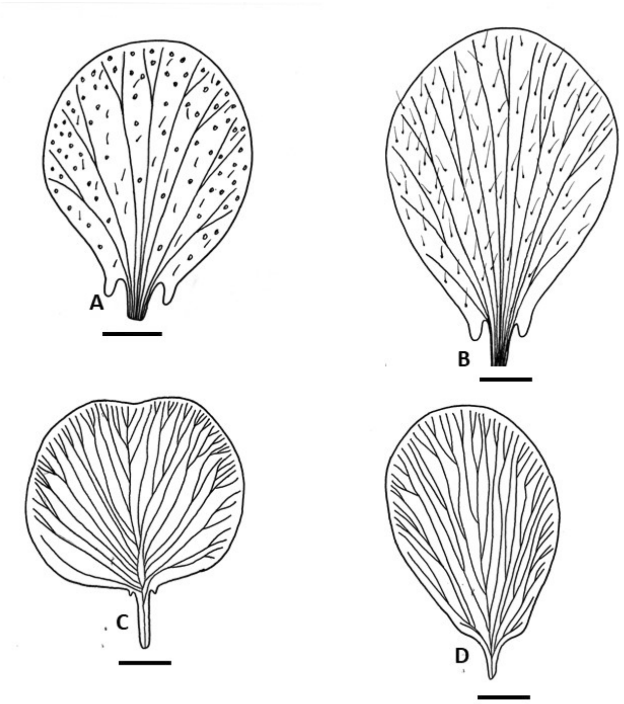

Figure 6. Variation in standard petals indumentum in *Rhynchosia* sect. *Rhynchosia* species. (A) Pubescent and glandular standard petal in *R. adenodes*. (B) Pubescent standard petal in *R. vendae*. (C) Glabrous standard petal in *R. bullata*. (D) Glabrous standard petal in *R. pauciflora*. Voucher specimens: (A) *Grobbelaar 1345* (PRE); (B) *Grobbelaar 02336* (PRE); (C) *Compton 11157* (PRE); (D) *Compton 27501* (PRE). Scale bar 1 mm**.** Drawn by Abdulwakeel Ajao.

subsp. *chrysadenia* var. *chrysadenia*, they are connate up to halfway while in *R. densiflora* subsp. *chrysadenia* var. *connata* they are connate more than halfway and sometimes to the apex (Jaca and Moteetee 2018). *Rhynchosia* sect. *Cyanospermum* and *R.* sect. *Polytropia* have upper calyx lobes connate to the apex while in *R.* sect. *Chrysoscias,* they are somewhat connate at the base.

Calyx indumentum varies from glabrescent to pubescent or pilose, villous to tomentose and glandular in the type section (Figure 5), it is pubescent or pilose and glandular-punctate in the *R. densiflora* group, pubescent, glandular-dotted in *R.* sect. *Polytropia* and entirely velvety canescent or sometimes brownish pubescent at base in *R.* sect. *Cyanospermum* (Moteetee et al. 2012; Moteetee et al. 2014; Jaca and Moteetee 2018; Jaca et al. 2018).

Standard petals

Species in the type section have standard petals that are persistent, yellowish, purplish to brownish or brown-maroon veined, with or without callosities, 5–18 × 4–21 mm, claw (0.5) 1–3 mm. It also varies in shape from ovate to obovate or cordate to orbicular or elliptic in the type section, suborbicular in *R.* sect. *Cyanospermum* and *R.* sect. *Polytropia*, ovate to broadly obovate in *R.* sect. *Chrysoscias* and elliptic to oblong in *R. densiflora* group (Moteetee et al. 2012; Moteetee et al. 2014; Jaca and Moteetee 2018; Jaca et al. 2018).

In terms of indumentum, the standard petals are glabrous and eglandular in all the sections and the *R. densiflora* group, with the exception of *R.* sect. *Rhynchosia* in which the standard petals are glabrous to pubescent or glandular. The indumentum on the standard petals is of great taxonomic importance as it can be used to separate morphologically similar species in this section. For example, *R. sublobata* and *R. caribaea* are similar in having deltoid or rhomboid leaflets, but the former can be differentiated by pubescent standard petals compared to glabrous in the latter. Also, *R. caribaea* var. *picta* can be differentiated from *R. caribaea* var. *caribaea* by its pubescent standard petals. Other species with pubescent and glandular standard petals in the type section are *R.*

adenodes, R, argentea, R. cooperi, R. crassifolia, R. galpinii, R. hirsuta, R. nitens, R. komatiensis, R. resinosa, R. spectabilis, R. vendae R. waterbergensis. In addition, *Rhynchosia pentheri* var. *pentheri* is occasionally glandular (Figure 6). Despite the absence of indumentum on standard petals in *R.* sect. *Chrysoscias,* its size is of diagnostic value. The standard petal is larger in *R. leucoscias* (10.0–15.5 × 7.0–15.0 mm) when compared to *R. microscias* (8–11 × 6–9 mm) and *R. leucoscias* (9.5–13.0 × 7.5–12.5 mm) (Jaca et al. 2018).

Wing petals

Oblong wings that are usually spurred at the base, 3–13 × 0.5–5.5 mm with linear claw 1–5 mm long is typical of the genus *Rhynchosia*. However, size, absence or presence of glands and surface sculpturing are of diagnostic importance. Wings are usually shorter than the keels in most of the species in the type section except in species such as *R. clivorum R. cooperii, R. ovata, R. resinosa* that have wings that are sometimes the same length as keel or even slightly longer than the keels as in *R. argentea*. Interestingly, in *R.* sect. *Chrysoscias,* the wing petals are equal to or longer than the keel petals in all species except in *R. microscias*, where they are slightly shorter than the keel. This character thereby separated *R. microscias* from the remaining species in the section (Jaca et al. 2018). Furthermore, the wings are generally longer than keels in *R. pinnata* and *R. smithiana* in *R.* sect. *Polytropia* (Moteetee et al. 2014). Most of the species in the genus have glabrous wings with the exception of *R. adenodes, R. albissima, R. atropurpurea, R. bullata,* and sometimes *R. pentheri* var. *pentheri* (all in the type section), which have glandular wings. Surface sculpturing can either be present or absent in the species in the type section and can be used to separate identical species. For example, *R. komatiensis* and *R. spectabilis* with similar ovate-orbicular or ovate leaflets, are distinguishable by the presence of sculpturing on the wings of *R. spectabilis*. Furthermore, *R. pauciflora* and *R. sp. nov.* are similar in having erect habit, linear or oblong leaflets and 1-flowered inflorescence. However, the former is separated from the latter by the presence of sculpturing on wing petals (Figure 7). The presence of surface sculpturing on the wing petals is also of taxonomic value in *R.* sect. *Polytropia* as it is used to distinguished *R. ferulaefolia* (where it is absent) from *R. pinnata* and *R. smithiana* (Moteetee et al. 2014). However, it is absent in *R.* sect. *Chrysoscias*, *R.* sect. *Cyanospermum*, and the *R. densiflora* group.

Keel petals

Keel petals are uniform in shape in the genus *Rhynchosia*, they are usually yellow, veined, pocketed, rostrate or boat-shaped, 5–15 × 2–9 mm, with a claw, 1–5 mm long. They are usually larger than the wings with the exception of those mentioned in the previous section and smaller than the standard petals. However, in *R. atropurpurea* the keels are almost the same length as the standard petals and entirely purplish colour, hence the specific name a*tropurpurea* (Figures 4C & 8). The colour of the keels in *R. atropurpurea* is the most important character to distinguish it from the remaining species in the genus.

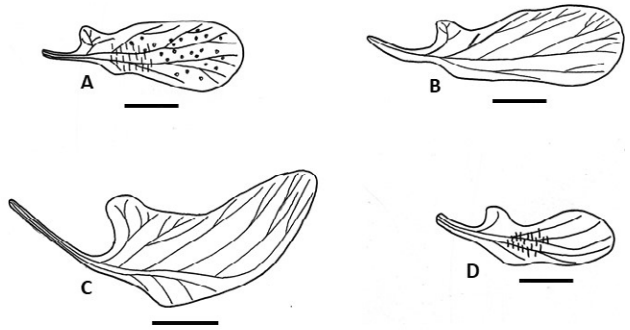

Figure 7. Variation in wing petals indumentum in *Rhynchosia* sect. *Rhynchosia* species. (A) Glandular with sculpturing in *R. adenode.* (B) Glabrous without sculpturing in *R. calvescens.* (C) Glabrous without sculpturing and narrow in *R. thorncroftii.* (D) Glabrous with sculpturing in *R. villosa.* Voucher specimens: (A) *Grobbelaar 1345* (PRE); (B) *Steyn 75* (PRE); (C) *Dlamini 3060* (PRE); (D) *Tyson 3085* (PRE). Scale bar 1 mm**.** Drawn by Abdulwakeel Ajao.

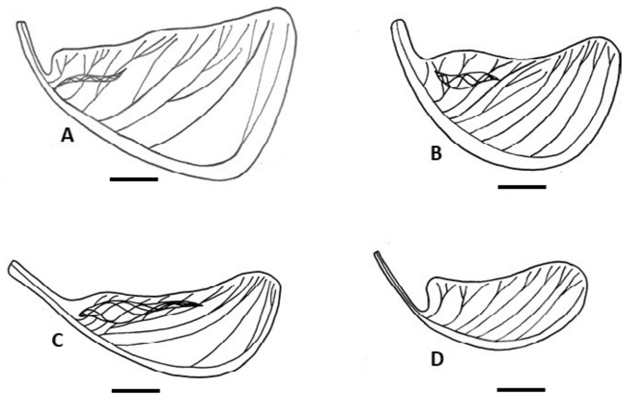

Figure 8. Variation in keel petals size in *Rhynchosia* sect. *Rhynchosia* species. (A**)** *R. atropurpurea.* (B) *R. arida.* (C) *R. nitens.* (D) *R. ovata.* Voucher specimens: (A) *Nkoane 33* (PRE); (B) *Van wyk 3029* (JRAU); (C) *Lansdell 16078* (PRE); (D) *Acocks 12979* (PRE). Scale bar 1mm**.** Drawn by Abdulwakeel Ajao.

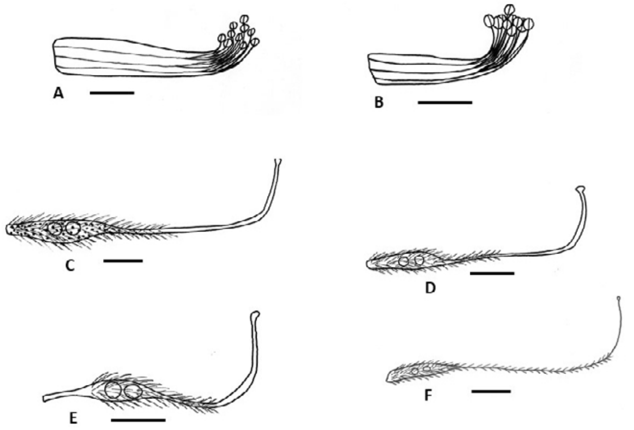

Figure 9. Variation in stamens and pistils in *Rhynchosia* sect. *Rhynchosia* species. (A) Stamens of *R. nervosa.* (B) Stamens of *R. reptabunda.* (C) Glandular and pubescent ovary in *R. capensis.* (D) Pubescent ovary in *R. calvescens.* (E) Stipitate ovary in *R. thorncroftii.* (F) Pubescent ovary with a very long style. Voucher specimens: (A) *Muller 1285* (PRE); (B) *Ngwenya 1337* (PRE); (C) *Vlok 708* (PRE); (D) *Steyn 75* (PRE); (E) *Dlamini 3060* (PRE); (F) *Nkoane 33* (PRE). Scale bar 1 mm**.** Drawn by Abdulwakeel Ajao.

Androecium

Stamens are uniform in the genus, and usually diadelphous with nine filaments fused and vexillary stamen free to the base. Anthers are also uniform, monomorphic, dorsifixed and somewhat dehiscent (Figures 9A-B).

Gynoecium

Ovaries are elliptic-oblong to oblong-lanceolate, sessile to subsessile or stipitate, puberulous or pubescent to pilose or glandular in *Rhynchosia* sect. *Rhynchosia*. However, they are narrowly oblong and subsessile in other sections but vary in terms of indumentum as it is densely silky-villous and glandular-punctate in the *R. densiflora* group and pubescent in *R.* sect. *Chrysoscias, R.* sect. *Cyanospermum,* and *R.* sect. *Polytropia* (Moteetee et al. 2012; Moteetee et al. 2014; Jaca and Moteetee 2018; Jaca et al. 2018). Styles are usually glabrous but sometimes pubescent to pilose or glandular most especially at the lower part. In the type section, it is usually 4–18 mm long and the variation in length can be of diagnostic importance. For example, *R.* a*tropurpurea* can be distinguished from *R. calvescens* by a longer style (13–15 mm) as opposed to the shorter style (7–10 mm) in *R. calvescens* (Figures 9C-D).

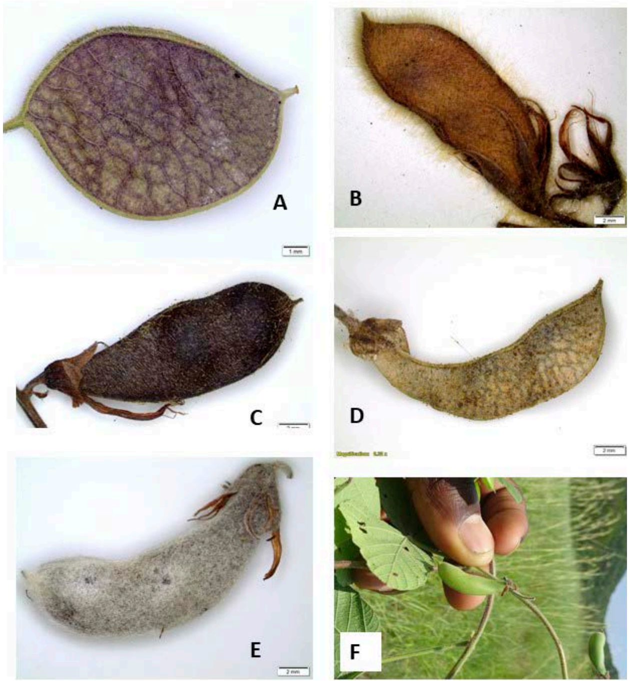

Figure 10. Variation in fruits in *Rhynchosia* sect. *Rhynchosia* species. (A) Elliptic, compressed or flattened in *R. monophylla.* (B) Oblong and pilose in *R. ovata.* (C) Oblong, stiped, pubescent and glandular in *R. adenodes* (D) Falcate, pubescent to tomentose and glandular in *R. emarginata.* (E) Oblong-falcate, canescent-tomentose in *R. albissima.* (F) Oblong-falcate, glabrescent, and inflated in *R. sublobata.* Voucher specimen: (A) *Nkonki 76* (PRE); (B) *Ward 4421* (PRE); (C) *Van Wyk 1589* (JRAU); (D) *Smook 7965* (PRE); (E) *Leendertz 484* (PRE). Photo by Abdulwakeel Ajao.

Fruits

The shape, size, and type of indumentum on the surface of the fruits vary greatly in the genus, but it can sometimes be of diagnostic importance. In the type section, fruits are 1–2-seeded, oblong to elliptic or falcate, 10–42 × 3–13 mm, compressed or inflated, stiped, glabrescent to pubescent or pilose to tomentose and glandular. It is important to note fruits of most species in this section are compressed and sometimes inflated as seen in *R. sublobata* (Figure 10F). In *R.* sect. *Cyanospermum*, the fruits are narrowly oblong, 2-seeded, 15–20 × 5–6 mm, densely velvety canescent or rusty-brown pubescent. However, they are oblong, broadly-oblong to ovoid, and 1–2-seeded in *R.* sect. *Chrysoscias* while they are narrowly oblong, 2-ovuled, densely silky-villous, and glandular-punctate in the *R. densiflora* group (Moteetee et al. 2012; Moteetee et al. 2014; Jaca and Moteetee, 2018; Jaca et al. 2018).

CONCLUSIONS

In this study, we investigated the reproductive and vegetative characters that can be used to delineate species within *Rhynchosia* sect. *Rhynchosia* and between the different sections in the genus *Rhynchosia* in southern Africa. The type section seems to more be variable, which might be due to the higher number of the species (47) as well as wider distribution in southern Africa when compared to the other sections. Within *Rhynchosia* sect. *Rhynchosia*, both vegetative and reproductive characters appear to be useful in the grouping of the species. These characters include growth habit, leaflet shape and indumentum as well as inflorescence length and type (branched or not), extent of connation of upper lobes of the calyx, indumentum on standard petals as well as presence or absence of surface sculpturing on the wing petals. However, structures such as stamen, pistil and keel petals are of lower taxonomic value as they tend to be similar within the section as well as between the sections. All the sections and the *R. densiflora* group overlap in terms of leaflet structure in that they all have either trifoliolate or unifoliolate leaflets with the exception of *R.* sect. *Polytropia* in which the leaves are trifoliolate to simply or pedately bipinnate, bi-tri-jugate, paucijugate, or supra-decompound. *Rhynchosia* sect. *Chrysoscias* and *R.* sect. *Polytropia* are morphologically related in that they both exclusively have lanceolate to linear-lanceolate leaflets. It is worth mentioning that these two sections are restricted to the Eastern and Western Cape Provinces (South Africa).

Flowers can either be solitary, sub-solitary (e.g., *R.* sect. *Chrysoscias*) on in axillary inflorescences which are either racemes or umbels. Reproductive morphological characters are more variable in the type section when compared to other sections. Standard petals indumentum varies from being glabrous to pubescent or glandular in the type section, but they are consistently glabrous and eglandular in all other sections including *R. densiflora* group. Although, *R.* sect. *Rhynchosia* and *R.* sect. *Polytropia* appear to be related when it comes to the presence or absence of surface sculpturing on the keel petals which are consistently absent in *R.* sect. *Arcyphylum, R.* sect. *Cyanospermum,* and *R. densiflora* group. However, *R.* sect. *Arcyphylum* is close to *R.* sect. *Cyanospermum* in the twinning growth habit and the many-flowered inflorescences which occur in dense subsessile axillary raceme. Morphologically, there are a number of overlapping characters between the sections, but we are not oblivious of the fact that Baker's sectional classification is natural. Hence the reason phylogenetic relationships were also investigated between the sections in the genus in this study to determine whether Baker's sectional classification will be upheld when using a combination of morphological and DNA sequencing data.

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Sempervivum guillemotii Lamotte (Crassulaceae), a rediscovered houseleek of the French-Italian Alps

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Abstract. S*empervivum guillemotii* (Crassulaceae) was discovered and described by Martial Lamotte in the French Alps, but apart from Rouy & Camus, it was never cited in the French floras. Burnat later rediscovered it, but unaware of Lamotte's name, he published it under the name *S. adenotrichum*; this name, too, did not find its way into the floras until the recent Flora Gallica. The author rehabilitates this name and designates a neotype for the name *S. guillemotii* and a lectotype for its synonym *S. adenotrichum*.

Keywords: Crassulaceae**,** *Sempervivum adenotrichum*, *S. guillemotii,* Western Alps.

INTRODUCTION

The genus *Sempervivum* L. (*Crassulaceae*) has been the subject of a great many studies, particularly in the nineteenth century, and a lot of taxa have been described especially in Austria, France, and Switzerland. Today there are hundreds of names, most of which are treated as synonyms; of these, very few being present in the major continental Floras. One of the most prolific and important authors of the period was Martial Lamotte (1820-1883), a French botanist who discovered and published a great many new species (Dayrat 2003). These include *Sempervivum guillemotii* Lamotte, the object of this study, which he described in detail. In particular, he highlighted its petal position at anthesis, its glabrous (or almost glabrous) stamens, a rare feature in the *Sempervivum* genus, and, rosette leaves which are glandular on the surface and have long (1 mm) cilia on their leaf margins (Lamotte 1856). Since its publication, *S. guillemotii* has been very rarely mentioned in the Euro-Mediterranean floras contexts and in France. Rouy & Camus (1901) treated this taxon simply as a 'forme' of *S. arvernense* Lecoq & Lamotte and, as a result, it was ignored by all subsequent Floras. Burnat (1906) later rediscovered it, but he was unaware of the earlier name published by Lamotte and published it as *S. adenotrichum* Burnat. No reference is made of this name in any major French Flora until Kerguelen (1999), who cites it as a synonym of *S. tectorum* L. subsp. a*rvernense* (Lecoq & Lamotte) Bellia & De Andrade, and Tison and Foucault (2014), who consider it a '[…] lignée fixée de *S.* ×*schottii* C.B. Lehm. & Schnittsp. (cf. Hybrides) […]' and later 'une espèce hybridogène'. In Italy, despite its widespread presence in the Piedmontese Cottian Alps, it does not appear in any Flora (Pignatti 1982; Gallo 2005; Gallo 2017; cf. also Gallo 2019). Likewise, *S. guillemotii* is not mentioned in Euro-Mediterranean contexts, such as the Euro+Med PlantBase (2006-). Recently, the Catalogue of Life (Roskov et al. 2018), cites it as a synonym of *S. tectorum* L. In the specialist literature, Correvon (1924) accepted the species, but its description lacks morphological diagnostic details. Praeger (1932) placed this taxon as a synonym of *S. tectorum*, while 't Hart et al. (2003) treated it as a synonym of *S. tectorum* var. *tectorum*.

The nomenclatural and taxonomic data related to this forgotten taxon are therefore very scarce and this study aims to explain the problem and restore the proper name for this taxon. To give stability and certainty to the name application, typifications of the name *S. guillemotii* and its synonym *S. adenotrichum* are provided.

MATERIAL AND METHODS

The morphological and biological characteristic of *S. guillemotii* and similar taxa were studied in the field (French and Italian Western Alps) and especially the type material of *S. guillemotii* and *S. adenotrichum* also in several herbaria (FI, G, GAP, LY, P and TO). Taxonomical and historical data were also investigated in the French and Italian literature. A comparison through statistical analysis (Anderson-Darling Normality test and paired t-test) of the altitudes of *S. guillemotii* and *S. montanum* L. subsp. *burnatii* (Wettst. ex Burnat) Hayek in Hegi, was performed with MaxStat®. The distribution map was created with SimpleMappr®. The distribution area will also be defined by integrating the distributional data used by Polidori et al. (2018), the exsiccata traced at G-BU and P, and the author's unpublished data. An analytical key, including morphologically similar taxa distributed in the same area is also proposed.

Taxonomy

In his protologue, Lamotte (1856) named the new species after M. [Monsieur] A. Guillemot (see Etymology), 'qui en a fait la découverte' and who sent the plants upon which the description had been based. It does not appear that this plant has been preserved but it was cultivated only, indeed there are no indications of its possible preservation in Lamotte's herbarium. The Lamotte herbarium is currently preserved at CLF (Dayrat 2003), and in a recent paper reporting the results of a study on the types contained in it, 11 specimens of *Sempervivum* were listed but no *S. guillemotii* (Roux 2010). This taxon is also missing from the remaining general herbarium of CLF (Roux *in litt.*). Likewise, the exsiccata collected by Lamotte are not traceable at FI and G. Indeed, it seems very unlikely that any herbarium specimens exist, since this same author states: 'Malheureusement, je ne puis la faire quant à présent, l'hiver de 1859-60 m'ayant fait périr ce que je possédais de ce *Sempervivum* sauf quelques petites rosettes qui n'ont pas encore donné de fleurs' (Lamotte 1864). Thus, Lamotte cultivated *S. guillemotii* for some years (Crépin 1865) but appears not to have prepared a specimen. This lack of original material forces the author to designate a neotype collected in the area where Guillemot gathered his material: the provenance selected is the Lac du Lauzanier, located in the area between Larche and Barcelonnette (Provence-Alpes-Côte d'Azur, France); here the author rediscovered this taxon in 2019.

S. adenotrichum was, on the other hand, described by E. Burnat based on specimens found in two different localities in the French Maritime Alps (Mont Férant and Cima della Fascia). Over his lifetime, Burnat built up a large herbarium kept separately at the Conservatoire de Botanique de Géneve as G-BU. The herbarium consists of more than 200,000 specimens, many of which are from the Maritime Alps (Jeanmonod & Charpin (2017). Studies aiming to typify names published by Burnat have already been carried out on this herbarium, the most important being Jeanmonod's study (2018). Here the author clarifies the best method with which to typify the names published by Burnat. There is almost always a complete coincidence - with respect to the presence of original materials - between the protologue and his herbarium. In Burnat's herbarium, two syntypes were found, corresponding to the localities listed in the protologue: one of these (Mont Férant, Fig. 2) was chosen as lectotype, because of a label written by J. Briquet (confirmed by D. Jeanmonod, *in litt.*) in 1903 and displaying the quote '*Sempervivum adenotrichum* Burnat et Briquet' (Figure 1B). On the other syntype, from 'Cima della Fascia', a small drawing can be observed depicting two 'Poils glanduleux des feuilles adultes (Figure 1A)', one of the diagnostic features of *S. guillemotii.*

Sempervivum guillemotii Lamotte in Communication. Bull. Soc. bot. France, 3: 457. 1856

Type: France. B.^{ses} Alp.^{es}. « Env. de Larche. (Le Lauzanier). Rive S. du Lac du Lauzanier. Alt.^{de} 2280^{m}. Roch-

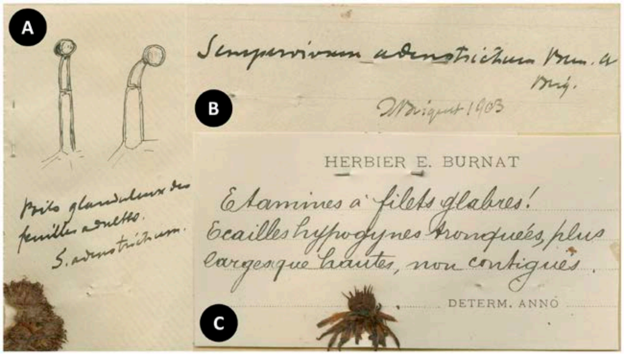

Figure 1. Details of the labels of the syntypes of *Sempervivum adenotrichum* Burnat. A. Drawing of E. Burnat, showing the glandular cilia on the leaf margins (G00848069). B. Label written by J. Briquet (Lectotype, G00848068). C. Label with morphological notes (Lectotype, G008488068).

ers. 15 Juillet 1949 ». *Laurence* (Herb. H. Laurence, P00321304, P [digital image at http://mediaphoto.mnhn.fr/media/1441344133347hfUgodcx0ryISleF]). Neotype here designated.

(=) *Sempervivum adenotrichum* Burnat in Fl. Alpes Marit. 4: 49. 1906
Type: France. Mont Férant, a l'W du M^t. Mounier. Rochers. Calcaire. 2000 m, *Burnat, Briquet, Cavillier, Verguin et Saint Yves*, 22/VII/1902 (G00848068, G-BU [Fig. 2]). Isolectotype G00848068a: Syntype: G00848069 (G-BU). Lectotype here designated.

Etymology

Dedicated to the French entomologist A. [Antoine] Guillemot (1822-1902) a butterflies specialist (Fournier 2015) See also: https://it.wikipedia.org/wiki/Antoine_Barth%C3%A9lemy_Jean_Guillemot).

Description and differentiation from similar taxa

Rosettes leaves erect or suberect, 30-100 (150) mm diameter. *Leaves* glandular on both faces, ciliate at the margins with glandular cilia (1 mm long); green or somewhat glaucous, (8)-10-(15) mm broad and (25)-30-(50) long, linear or obovate with brown or violet apex. No smell of resin. *Inflorescences* strong, (12)-20-(30) cm long, glandular; compact not scorpioid. *Flowers* rounded in the bud and densely glandular. *Petals* (11)-12-(15), linear, reflexed toward the apex (decumbent) or twisted with a hooked tip, light or dark pink, with a green central line and violet spots of varying size; (10-) 12-14 (-15) x (1-) 1,5-2,5 (-4) mm. *Carpels* erect, green, glandular at least on the ventral side, but often throughout with transparent or red (Vallée de la Tinée, France) glandules. *Styles* red-violet erect or somewhat outwards. *Filaments* violet, glabrous at the base or with 1-2 glandular hairs. *Anthers* (before dehiscence) violet sometimes bronze, with or without mucro. *Nectary scales* quadrangular, transparent or slightly permeated with yellow, apex retuse or flat.

Figure 2. Lectotype of *Sempervivum adenotrichum* Burnat (G00848068, G-BU (Photo: Conservatoire Botanique de Géneve, G-BU).

S. guillemotii coexists, with *S. arachnoideum* L., *S. tectorum*, *S. montanum* subsp. *burnatii* Wettst. ex Hayek and a hybrid of the last two (= *S. ×schottii* C.B. Lehm. & Schnittsp., according to a part of the current literature e.g. Praeger 1932, Jacobsen 1977, Gallo 2019) and can easily be confused with these. The characteristic presence of glandular hairs on the leaf faces and cilia on the leaf margins (often glandular) excludes the two putative parents. *Sempervivum guillemotii* can be distinguished from the hybrid by means of the filaments: glabrous or (rarely) with 1-2 glandular hairs in *S. guillemotii* but very glandular in the hybrid (see the analytical key). The guidance provided by Lamotte (1856) on the glandulosity of the filaments "Etamines [...] légèrement hispidulesglanduleux à la base [...]” is very unclear but, from what was seen in the field by the author can be quantified as not more than 1-2 glandular hairs per filament. Furthemore, the frequency of occurrence in the wild varies significantly: in agreement with Polidori et al. (2018), *S. tectorum* and *S. montanum* hybrids occurs as scattered specimens, usually near their parents (cf. Gallo 2001). *S. guillemotii* forms, quite often large populations, sometimes with giant clumps of rosettes some of which attain considerable size, and often in the absence of at least one of the two putative hybrid parents.

Analytical key to distinguish S. guillemotii *from other similar taxa present in the area studied*

1. Leaves glandular on the margins and scented of resin, petals violet (rarely pink or in part yellow), whitish the margins.. ***S. montanum*** subsp. ***burnatii***

   Leaves with cilia at the margins, no smell, petals never violet 2

2. Leaves glabrous throughout, petals white-pink, 10-11 mm long .... ***S. tectorum***

   Leaves glandular on both faces, petals dark rose or red-violet, petals longer than *S. tectorum* 3

3. Filaments very glandular, rare and isolated plants .... ***S.*** × ***schottii***

   Filaments glabrous or (rarely) with 1-2 glandular hairs, populations with many plants .... ***S. guillemotii***

The analytical key must be considered a rough tool to identify taxa with similar morphological features growing in the Maritime-Cottian Alps. However, it must be borne in mind that, hybridization occurs very easily in the *Sempervivum* genus and is well known (Loret 1858; Baker 1879; Vaccari 1905; Praeger 1932; Favarger et al. 1968; Favarger 1969; Favarger; 1971; Rowley 1982; Gallo 2001; ‘t Hart et al., 2003; Gallo 2012), and hybrids are often not easy to distinguish from its parents. During the research in the field, I found plants that could be interpreted as *S. guillemotii* hybrids with other taxa such as *S. montanum* subsp. *burnatii* or also *S. arachnoideum* several times (see also Polidori et al. 2018), but to date it has not been possible to identify them unequivocally. Further study in this regard is already underway.

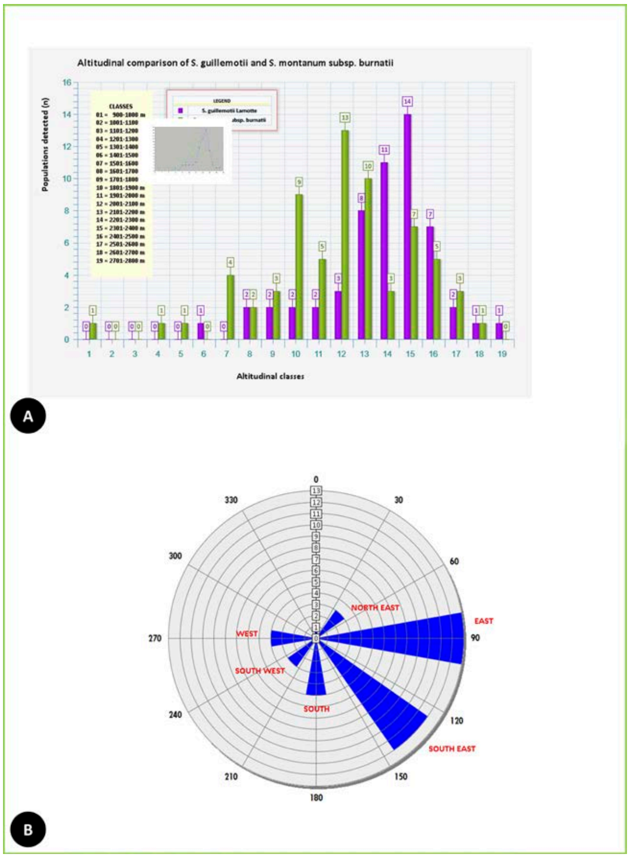

Figure 3. Ecological data related to *Sempervivum guillemotii*. A. Comparison of the altitudes of *S. guillemotii* Lamotte and *S. montanum* L. subsp. *burnatii* Wettst. ex Hayek. B. Exposure of *S. guillemotii* as found in the field.

Habitat

S. guillemotii occurs in pastures among rocks and debris, where vegetation is absent or very scarce, in full sun, more rarely in tall grass. In one case it was found on the top of a stone wall but had probably been cultivated there. Its habitat is often sloping and south or east facing (Figure 3B) (see also Polidori et al. 2018). Perhaps, *S. guillemotii* is a somewhat sensitive to cold winters, and probably also to long-lasting snow. This species has been found from 1400 m, in Vallée de la Tinée (France), to 2714 m, in Valle Maira. Figure 3A gives a comparison between the altitudes – as seen during field trips - between *S. guillemotii* and *S. montanum* subsp. *burnatii*, with which it often coexists in the same area. *S. guillemotii* is frequent especially between altitudes of 2100 and 2500 metres (classes 13-16) while it is rare at both lower and higher altitudes (classes). The distribution of the two frequencies, evaluated with the Anderson-Darling Normality test, is normal. Conversely, no significative difference appears between the altitudes reported for the two species: the paired t-test was not positive (T=0.681, p-value = 0.5047, $P<0.05$, significance level 95%), although *S. montanum* subsp. *burnatii* was detected at a lower altitude and presented a ‘distributive

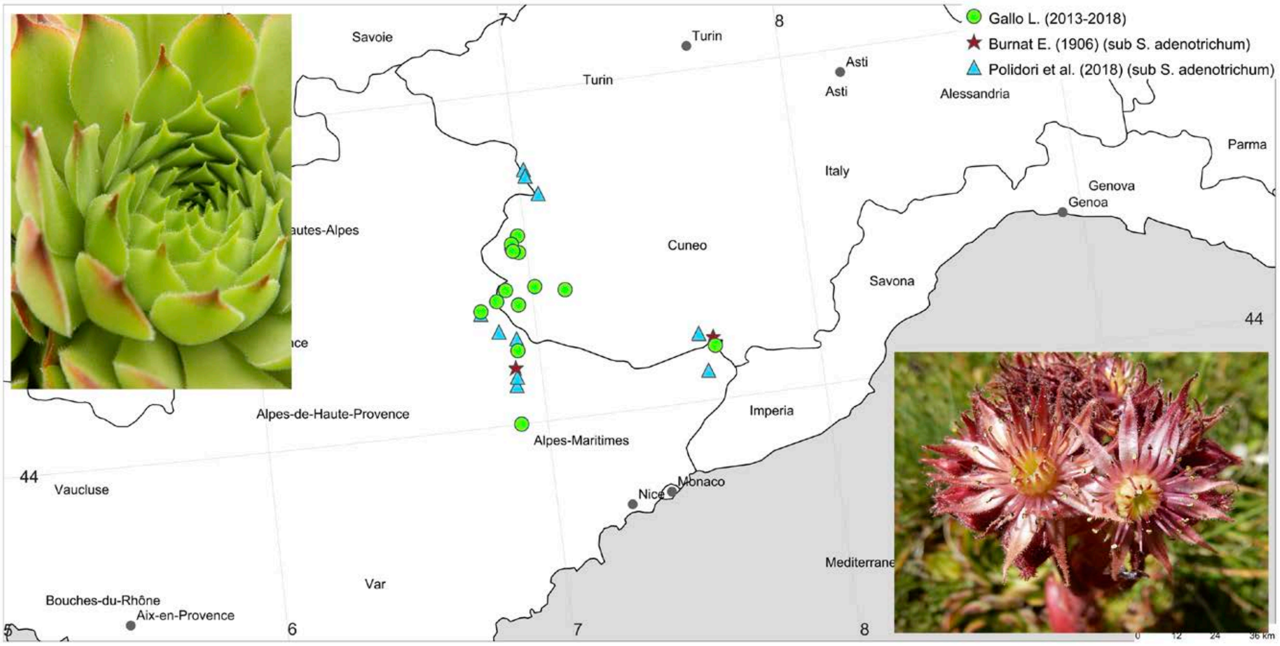

Figure 4. Distribution area of *Sempervivum guillemotii* Lamotte (incl. *S. adenotrichum* Burnat).

queue' which was wider to the left. Polidori et al. (2018) also report an empirical study evaluating the pH value of the ground at the level of the roots in the French Maritime Alps, obtaining a range of values, roughly 5 to 7; these data however, appear inconsistent with what Burnat writes (1906: 49): 'Sur les lieux mêmes nous avons noté que le soil étatit calcaire dans les deux cas […]'.

Distribution area

S. guillemotii is currently considered to be endemic in the Western Alps (Figure 4), but possible disjunct populations discovered in non-Alpine French areas, currently under investigation, have complicated the issue concerning its origin. In France, where the species was discovered, it is mainly to be found in the Maritime Alps (Polidori et al. 2018) but some northerly populations have been found in the Queyras (Hautes-Alpes); the author found it also in Ubaye, Vallée de la Tinée, Val Roya and Lauzanier. In Italy, the first published report is from the neighbourhood of Limone Piemonte (Val Vermenagna) (cf. Bellone in Polidori et al. 2018) but this identity was already ascertained in 2013 (see *Additional specimens examined*) although it had been gathered many years before (see appendix 1). Its current Italian distribution includes the Cottian Alps (Val Grana, Val Maira and Val Varaita) and Maritime Alps (Val Stura). See the appendix 1 for a list of living specimens studied.

Origins

The origins of *S. guillemotii* are obscure, a genetic mutation or an ancient hybridization can be supposed. Burnat (1906) (*sub S. adenotrichum*) assumes that the parents were *S. tectorum* and *S. montanum*, but a lack of other taxa in the area made it impossible for him to verify this hypothesis. Tison and Foucault (2014) (*sub S. adenotrichum*) treat it as a hybrid between *S. tectorum* and *S. montanum*, found from the Maritime Alps to Valle d'Aosta. These French authors do not distinguish, between *S. guillemotii* and the casual hybrid (= *S.* ×*schottii*), which should be kept distinct, especially because the origin of *S. guillemotii* might be different from that of *S.* ×*schottii*. The hypothesis that it is a successful natural hybrid (or also allopolyploid) is credible whereas it is much more difficult to identify the parents; while *S. guillemotii* could be a hybrid between taxa belonging to the groups of *S. tectorum* and *S. montanum*, it is not necessarily true that the parents are these two species *sensu stricto*.

Phenology

The anthesis is in July, the pollination is entomophilous as is usual in the genus *Sempervivum*; the flowering and the consequent production of seeds is erratic since the formation of inflorescences, in many of the studied populations, lacks in some years.

Iconography

Polidori et al. (2018); Gallo (2019).

Additional specimens examined

ITALY: Piedmont. Cuneo, Valle Maira, Vallone di Unerzio, From Prato Ciorliero to Passo Gardetta. 2181 m, W. Grassland among calcareous rocks. 339916N, 4920648E. *Gallo*, 14/07/2013 [*GL-8004/2*] (8220/ 11.2018, TO).

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APPENDIX 1. LIVING SPECIMENS STUDIED BY THE AUTHOR

France (P.A.C.A.). Vallon Lauzanier, Lac du Lauzanier towards Pas de Cavale, debris with *Sedum alpestre*, *Daphne sp.*, *Hylotelephium anacampseros*, *Veratrum album*, *Adenostyles* sp. ecc. 2353 m, E, 0330236 E, 4915588 N (GL-8437, 8440, 8860, 8861 8864, 8 July 2019). Between Colle della Boaria and Rif. Morgantin, calcareous rocks, 2181, SE (GL-4538). Vallée de la Tinee, Circuit de la Tortisse da le Prà au Lacs de Vens, pasture, 2260 m, 0334656 E, 4909146 N (GL-7408, 10 August 2011). Vallée de la Tinée, between St. Etienne and Auron, in the scrubland with *Buxus sempervirens,* 1400 m., 0336314 E, 4899070 N (GL-7377, 8 August 2011). Vallée de la Tinée, Auron, hill above the parking among the shrubs, with *Juniperus* sp. e *Lavandula* sp., 1691 m, 0334301 E, 4898893 N (GL-7379, 7382, 8 August 2011). Vallée de la Tinée, Col de la Bonette, under the summit, pasture, 2611 m (0326434 E, 4911160 N (GL-7386, 9 August 2011). Ubaye, Vallone Fouillouse toward Col du Vallonet, moraine in the valley, pasture with rocks with *Vaccinium myrtillus* and *Dryas octopetala,* 2295 m, 0683346 E, 4450245 N (GL-8735, 23-26 July 2018). **Italy (Piemonte, Cuneo).** Val Maira, between Viviere and Colle Ciarbonet (Baite Rosano), rocks, 2075 m, L. Gallo obs. 31 July 2001. Val Maira. Vallone Traversiera from Madonna delle Grazie to Rif. Carmagnola, pasture 2365 m, 0377252 E, 4932191 N (GL-8107, 10 luglio 2014). Val Maira, Vallone Maurin, Refuge D. Sartore, pasture with rocks, 2444 m, 0332569 E, 4927464 N (GL-8222, agosto 2014). Val Maira, Vallone Maurin, trail for Colle Bellino from the parking, pasture with rocks near the chalets, 2201 m, 0334411 E, 4933377 N (GL-8476). Val Maira, Vallone Maurin, trail for Colle Bellino, pasture with rocks, 2248 m, 0334638 E, 4933540 N (GL-8478). Val Maira, Vallone Maurin, trail for Colle Bellino from the parking, pasture with rocks, 2350 m, SE, 0334759 E, 4933892 N (GL-8479, 8480). Val Maira, Vallone Maurin, trail for Colle Bellino from the parking, pasture with rocks, 2247 m, S, 0334445 E, 4933588 N (GL-8481). Val Maira, Vallone Maurin, loc. Saretto towards refuge D. Sartore - Fonte Baciasse, pature, 2349 m, E, 0332791 E, 4927489 N (GL-8217, august 2014). Val Maira, Vallone Maurin, loc. Saretto toward refuge D. Sartore - Fonte Baciasse, pasture with rocks, 2192 m, 0333198 E, 4927417 N (GL-8211, 8212, 8213, 8214, august 2014). Val Maira, Vallone Maurin, Between Colle Greguri and Colletto, on the trail near the 'Fortino dei cavalli', pasture with rocks, 2438 m, NW 0335256 E, 4931314 N (GL-6786). Val Maira, Vallone Traversiera, towards Colle di Traversiera, under N. Freide/Aubrage, pasture, 2247 m, SW, 0338410 E, 4931423 N (GL-8199, august 2014). Val Maira, Vallone Traversiera, towards Colle di Traversiera under N. Freide/Aubrage, pasture with rocks, 2260 m, E, 0338320 E, 4931479 N (GL-8193, august 2014). Val Maira, Vallone Traversiera, from Madonna delle Grazie towards Rif. Carmagnola, 2458 m, 0336919 E, 4933219 N (GL-8572, July 2016). Val Maira, Vallone Traversiera, from Madonna delle Grazie towards Rif. Carmagnola, 2507 m, 337056 E, 4933777 N (GL-8573, July 2016). Val Maira, Vallone Traversiera, from Madonna delle Grazie towards Rif. Carmagnola, 2714 m, 0337044 E, 4934652 N (GL-8576 July 2016). Val Maira, Vallone Traversiera, from Madonna delle Grazie towards Rif. Carmagnola, 2345 m, 0337420 E, 4932378 N (GL-8569, July 2016). Val Maira, Vallone Traversiera, from Madonna delle Grazie towards Rif. Carmagnola, 2388 m, 337153 E, 4932635 N (GL-8570 July 2016). Val Maira, Vallone Traversiera from Madonna delle Grazie towards Rif. Carmagnola, pasture, 2365 m, 0377252 E, 4932191 N (GL-8106, 8108, 8109 10 luglio 2014). Val Maira. Vallone Traversiera, from Madonna delle Grazie towards Rif. Carmagnola, wall, 2164 m, E, 0338700 E, 4931253 N (GL-8118 10 July 2014). Val Maira, Vallone Traversiera from Colle di Traversiera under N. Freide/Aubrage, pasture, 2250 m, NE, 0338596 E, 4930959 N (GL-8189, August 2014). Val Maira, Vallone Traversiera from Madonna delle Grazie towards Rif. Carmagnola, rocks in the pasture, 2363 m, NE, 0337334 E, 4932183 N (GL-8104 10 July 2014). Val Maira, Vallone Traversiera toward Colle di Traversiera under N. Freide/Aubrage, pasture and debris, 2162 m, E, 0338729 E, 4931007 N (GL-8205, August 2014). Val Maira, Vallone Traversiera from Madonna delle Grazie towards Rif. Carmagnola, pasture, 2370 m, 0337174 E, 4932257 N (GL-8111, 10 July 2014). Val Maira, Vallone Traversiera from Madonna delle Grazie towards Rif. Carmagnola, pasture, 2365 m, 0337174 E, 4932257 N (GL-8112, 8113, 10 July 2014). Val Maira, Vallone Traversiera towards Colle di Traversiera under N. Freide/ Aubrage, pasture, 2213 m, 0338506 E, 4931356 N (GL-8200, 8202, August 2014). Val Maira, Vallone Traversiera from Madonna delle Grazie towards Rif. Carmagnola, rock pasture, 2417 m, E, 0337011 E, 4932517 N (GL-8116 10 July 2014). Val Maira, Vallone Unerzio, from Viviere towards Colle Ciarbonet, rocks, 1852 m, E (GL-5274). Val Maira, Vallone Unerzio, from Viviere towards Colle Ciarbonet, wall, 1939 m, (GL-5280). Valle Stura, towards Colle Seroup, pasture with rocks, 2476 m, E, (GL-4938, 4939). Valle Stura, Vallone Arma, from Colle di Valcavera towards Cima di Test, pasture with rocks, 2454 m, SE (GL-4803). Val Stura, Vallone Arma, above S. Giacomo, pasture with rocks, 1735 m, SW (GL-4733). Val Stura, Vallone Arma, above S. Giacomo, debris, 2331 m, E (GL-4734). Val Stura, Vallone del Piz from Bersello, vallone di Ferrere above Ferrere towards Gias Colombart, pasture, 2189 m, 0335111 E, 4914128 N (GL-8549, 8550). Val Varaita, Vallone Bellino, from Rif. Melezet towards Pian di Traversagn, pasture with rocks, 1998 m, NE, 0697391 E, 4456753 N (GL-8673).

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Monitoring of alien aquatic plants in the inland waters of Sicily (Italy)

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Abstract. Updated and reliable data on the presence and distribution of alien aquatic plant species in Sicily are lacking, and there is a need to fill this gap for a proper and efficient management of freshwater ecosystems and biodiversity. This paper reviews the available knowledge about alien aquatic vascular plants in the inland waters of Sicily (Italy). The aim is to provide an updated checklist, as a first step in the study of the impact of those plants on the native species and ecosystems of this Mediterranean island. The paper focuses on the strictly aquatic species (hydrophytes), excluding emergent macrophytes. Four species were listed, all of them free-floating and with American origin. Most of them occur within protected areas, and their introduction in the island appears to be anthropogenic. A set of functional traits of the alien species, such as relative growth rate, leaf mass per area, nitrogen and carbon content, were screened. These traits are useful for assessing the species invasive potential compared to native ones.

Keywords: alien species, aquatic plants, biodiversity, functional traits, hydrophytes, protected areas.

INTRODUCTION

Invasive alien species pose a major global threat to the conservation of biodiversity, causing the extinction of native species and modifying ecosystem functions: this is true also for aquatic habitats, particularly susceptible to invasion due to usually high disturbance regimes affecting these habitats and the easy dispersal of water plant propagules. In addition, aquatic environments are also difficult to monitor, and an early detection of introduction of a submerged species is seldom possible (Brundu 2015).

Mediterranean islands are particularly appreciated model systems for studying invasions due to the diversity of alien taxa, long history of species introductions and (usually) detailed floristic records (Hulme 2004; Lloret et al. 2005; Bjarnason et al. 2017; Chiarucci et al. 2017; Pasta et al. 2017).

The island of Sicily is one of the main hotspots of plant biodiversity, in the center of the Mediterranean basin (Médail and Diadema 2009), housing more than 3,000 wild plant species (Pignatti et al. 2017-2019) and being an ideal stage for research in ecology and evolution (e.g. Geraci et al. 2009, 2019; Minissale and Sciandrello 2016); it hosts different types of freshwater habitats, both lentic (coastal wetlands, temporary ponds, lakes, reservoirs) and lotic (springs, streams, permanent and seasonal watercourses) (Gianguzzi et al. 2016), with many endemic or endangered species occurring in aquatic habitats (cf. Bonanno and Veneziano 2011; Troia et al. 2012; Troia and Lansdown 2016; Sciandrello et al. 2016; Minissale et al. 2017).

In the last years new aquatic alien species, such as *Lemna minuta* Kunth (Marrone and Naselli-Flores 2011), and new populations of already reported ones, such as *Eichhornia crassipes* (Mart.) Solms (Ferro 2013), have been reported. Nevertheless, no recent and updated synthesis on the ecology and the distribution of the Sicilian alien aquatic flora is currently available.

Thus, the aims of this work were i) to compile data on the distribution of alien vascular plant species with special reference to their occurrence in protected areas, as a first step in the analysis of the effects of the alien species on the aquatic habitats of the island; ii) to compile data on some functional traits (such as relative growth rate, leaf area, leaf mass per area, nitrogen and carbon content) of the alien species, in order to allow predictions about their potential invasiveness of natural wetlands.

MATERIALS AND METHODS

In the literature, the term ‟water plant" has usually been applied rather arbitrarily in the case of plants occurring in and near the water (cf. Brundu 2015); here we refer to the classification of Chambers et al. (2008), framing the aquatic plants in four main groups: emergent macrophytes (plants that are rooted in submersed soils or soils that are periodically inundated, with foliage extending into the air), floating-leaved macrophytes (plants rooted to the lake or stream bottom with leaves that float on the surface of the water), submersed macrophytes (plants that grow completely submerged under the water, with roots or root analogs in, attached to, or closely associated with the substrate), and free-floating macrophytes (plants that typically float on or under the water surface). In particular, in this study we focused only on the vascular plants belonging to the last 3 types (“hydrophytes” according to Raunkiaer 1934), so excluding the not-strictly aquatic plants. In this sense, our three categories correspond to the three groups adopted by the European and Mediterranean Plant Protection Organisation (EPPO) (EPPO 2014).

Inland waters are here defined according to the Water Framework Directive (Directive 2000/60/EC), excluding transitional waters.

Finally, alien species are here defined as “plant taxa in a given area (…) whose presence there is due to intentional or unintentional human involvement, or which have arrived there without the help of people from an area in which they are alien” (Pyšek et al. 2004).

We consulted all available literature regarding the alien flora in Sicily, to prepare a list of the alien aquatic vascular plants reported for the island, with family names and order according to Smith et al. (2006) and Haston et al. (2009). In addition, databases and photographs from popular websites such as Acta Plantarum (www.actaplantarum.org) have been consulted to obtain recent data and cover under-represented geographic areas. Finally, the management plans for the “Natura2000 sites” (protected areas designated according to the European ‘Habitats’ Directive 92/43/CE, which mostly overlap with natural parks and reserves), available on the website of the Sicilia Region (http://www.artasicilia.eu/old_site/web/natura2000/index.html), were consulted, too.

We reviewed the scientific literature published in the last fifteen years (2006-2020) to screen the most relevant physiological traits that may aid in assessing the invasive potential of alien species compared to native ones. Literature search was made in the Scopus and Google Scholar databases, using as keywords the names of the species resulting from the list compiled as described in the previous paragraph.

RESULTS

Four aquatic alien species (Table 1), belonging to 3 genera and 3 different families, including both ferns (2 species) and angiosperms (2 species), are reported for Sicily.

About *Azolla*, the taxonomy of this genus “is difficult and controversial since the vegetative and some reproductive characters used to identify these species are highly variable, depending on the collection site and on the environmental conditions” (Pereira et al. 2011). In addition, nomenclatural reasons linked to the use of the name “Azolla caroliniana” created further confusion, so that the two species previously reported for Sicily (Romano et al. 1994) have been considered a single species in the last national Flora (Pignatti et al. 2017-2019). According to some recent studies (e.g. Evrard and van Hove 2004; Lastrucci et al. 2019), two different species occur in Sicily: *Azolla filiculoides* Lam. and *A. cristata* Kaulf. (= *A. carolinana* sensu Auct.) (Table 1).

Table 1. List of the alien aquatic vascular plants reported for Sicily.

Species	Family	Origin	Number of known populations in Sicily	Number of populations within a protected area	**References**
Azolla filiculoides Lam.	Salviniaceae	America (N&S)	3	2	Romano et al. 1994; Albano 2010; Giordana 2013
Azolla cristata Kaulf. (= *Azolla mexicana*) (= *Azolla caroliniana* Auct. non Willd.)	Salviniaceae	America (N&S)	2	2	Romano et al. 1994; Minissale and Sciandrello 2017
Lemna minuta Kunth	Araceae	America (N)	1	1	Marrone and Naselli-Flores 2011
Eichhornia crassipes (Mart.) Solms	Pontederiaceae	America (S)	3	2	Bartolo et al. 1976; Ferro 2013; Di Gregorio 2014

Table 2. Functional traits of the 4 alien aquatic species reported for Sicily.

	LA mm^2	LMA mg mm^{-2}	RGR g g^{-1} d^{-1}	NC %	CC %	
Azolla filiculoides	0.9-0.92	0.003-0.024	0.08-0.9	2.01-3.5	35.4-42.5	Brouwer et al. 2018; Cheng et al. 2010; Gufu et al. 2019; Lukàcs et al. 2017; Pierce et al 2012; Shaltout et al. 2012; Van Kempen et al. 2016
Azolla cristata (= *Azolla mexicana*) (= *Azolla caroliniana* sensu Auct.)			0.09-0.18	4.0		Hassan et al. 2020; Lizieri et al. 2011; Roberts et al. 2014; Rofkar et al. 2014
Lemna minuta	2.4-3.07	0.008-0.01	0.16	2.37-2.7	35.3-41	Pierce et al. 2012; Gérard & Triest 2014; Lukàcs et al. 2017
Eichhornia crassipes	3500-7300	0.05-0.07	0.002-0.045(2)	2.2-2.5	40	Henry-Silva et al. 2008; Fan et al. 2013; Wang et al. 2017; Eid & Shaltout 2017; Zahoor et al. 2018; Upadhyay & Pame 2019; Wauton & William-Ebi 2019

Abbreviations: LA, leaf area; LMA, leaf mass per area; RGR, relative growth rate; NC, nitrogen content; CC, carbon content.(1) average of different clones. (2) different nutrient availability or growth sites.

The presence in Sicily of another species, which we did not include here, *Halophila stipulacea* Asch. (Hydrocharitaceae) (Biliotti and Abdelahad 1990), is noteworthy; although it is a seagrass, native to the Indian Ocean and reported for the coasts of Sicily, it seems able to colonize also coastal ponds with salt or brackish water (Procaccini et al. 1999), potentially threatening protected areas such as "Saline di Trapani e Paceco", "Stagnone di Marsala" and similar areas including saltworks and lagoons.

Table 1 shows that 4 out of 4 species are of American origin, all of them coming from warm, subtropical or tropical areas. This latter circumstance can be explained with the Mediterranean climate occurring in Sicily; the former one is probably to be linked to the reasons reported in the next paragraph. Interestingly, also the 10 alien hydrophytes reported for Sardinia (Mayoral et al. 2018) are American species.

Considering the geographic origin of the species, and their use in many human activities, it seems probable that *Homo sapiens* is the main vector of their introduction: all of these species are in fact commonly used as ornamental plants in gardens, fish tanks and aquaria, or as effective living elements in constructed wetlands (see Mazza et al. 2015).

All the aquatic alien species occurring in Sicily are free-floating species. Other alien aquatic species with a different growth-form potentially occurring in Sicily, for example the rooted *Elodea canadensis* Michx. and *Myriophyllum aquaticum* (Vell.) Verdc. (occurring in northern and central Italy), have not been found (till now at least), probably for climatic reasons.

Practically all the sites in which alien aquatic species were reported are located within protected areas (Table 1), i.e. natural parks and reserves or sites of the Natura2000 network (but also in an archaeological park). These areas include both coastal habitats (such as wetlands and river mouths) and lakes and ponds in the hills, not far from the coast.

Available literature from the last fifteen years often reported different traits for the alien species found in Sicilian wetlands. The functional traits that could be most widely compared among these species are reported in Table 2. We did not find recent data for *Azolla cristata* in our literature survey: considering the nomenclatural matters cited above, we included in Table 2 data for *A. caroliniana* (*sensu lato*). *Eichhornia crassipes* was the species with the highest leaf area and leaf mass per area (LMA) values. The lowest LMA values were reported for *Lemna minuta*, mainly reflecting the different leaf morphology between the species. Relative growth rate in *Eichhornia crassipes* was lower than the maximum RGR reported for the other species. Tissue nitrogen content was higher for the *Azolla* species, as predictable. Available data on carbon content, instead, were quite similar among the different species.

DISCUSSION

Comparing the number of alien aquatic plant species reported for Sicily with the total number of alien aquatic plant species in the EPPO list (Brundu 2015) - even if it does not include some of the species in our list - reveals that about 1/5 of that number have been found in Sicily, on a very limited area compared to the EPPO region currently including 50 countries (www.eppo.int). However in Sardinia, another Mediterranean island geologically different from Sicily but similar for climate and size, the number of alien hydrophytes is more than double (Mayoral et al. 2018).

The alien aquatic species here reported seem to be limited to few localities, so it seems they are not invasive; but really the feeling is that we have too scarce information – and scattered in time - to say something about their real status.

Our results show that aquatic alien species in Sicily have been reported almost exclusively from protected areas. This probably because protected areas are better studied and monitored, compared to other non-protected areas, and so they can function as ‘sentinels’ for monitoring the spread of invasive aquatic plant species. But this means also that: 1) the presence of (potentially invasive) alien species in protected areas must be managed (see for example threats and priorities for alien plant invasions in protected areas in Foxcroft et al. 2017); 2) Probably, other populations (and other species?) of alien plants could be already present in “secondary” and overlooked aquatic habitats, outside protected areas.

Usually, monitoring of invasive plant species focuses on terrestrial habitatas. During the preparation of the management plans of the Natura2000 sites in Sicily, that were made in the same period all over the island about 12 years ago, special attention to alien invasive species was asked by Regional Coordinators: only in one (Albano 2010) of the 25 examined plans a single aquatic invasive plant species is mentioned.

The situation we found in Sicily for aquatic alien species fits well (unfortunately) with the general lack of information on the presence and abundance of invasive aquatic plants in protected areas in all Mediterranean islands, as highlighted by Brundu (2013), who defined this a serious hindrance for management at international levels.

In the case of alien aquatic species in Sicily, we have seen that their introduction is generally linked to their use and release (intentional or not) by man. The release of alien species in natural habitats is generally prohibited by law, but in Italy, as in several other countries, this is not sufficient to avoid the diffusion of potentially invasive plants. While the impact of alien species on the native aquatic systems of Sicily is well known as regards the faunistic aspects (Marrone and Naselli-Flores 2015), it still has to be evidenced for floristic aspects.

The identification of a general set of functional traits favoring invasiveness may be controversial, as traits of invaders depend on many factors, among which reproductive strategies (Violle et al. 2007), ecological and physiological traits of native species and the environmental conditions of invaded habitats (Funk 2013). Generally, native species are the ones best adapted to a given habitat, but the arrival of alien, more competitive species may alter the ecosystem balance, especially when perturbations of that habitat occur. For terrestrial habitats, many studies have reported differences in morphological or physiological traits between native and invasive taxa, while others have not proved the predictability of invasiveness from these traits (Leffler et al. 2014).

In aquatic environments, an important factor determining invasiveness is nutrient availability. For example, experiments comparing competitiveness between *Lemna minuta* and *L. minor* found that the invasive species was dominant only under high levels of nutrient availability (Njambuya et al. 2011), and therefore invasion would increase with eutrophication, as reported also for *E. crassipes* (Coetzee et al. 2017) In mixed aquatic communities, plant density has been reported as another relevant factor affecting invasiveness, either through facilitation or competition, depending on the species (Silveira and Thiébaut 2020).

LMA is a trait central to the pattern of the leaf economic spectrum, which shows a negative correlation with photosynthetic rate across species (John et al. 2017). High values of LMA are typically found in slow growing species, while low values are common for fast growing species (Wright et al. 2004; Reich 2014). Most hydrophytes share low LMA values, a trait related to high resource acquisition strategies that may aid in competition (Pierce et al. 2012), so invasive species with lower LMA than native ones may be at advantage.

It is clear from this first analysis that updated and complete data on the presence of alien aquatic species in Sicily and on their competitiveness with native species are lacking, so there is the need to fill this gap for a proper and efficient management of ecosystems and biodiversity. Conservation of wetlands remains particularly challenging, given the importance of fresh water for human communities and the consequent pressure wetlands and water bodies are prone to, and this type of ecosystems can no longer be considered the "poor cousins" (Kingsford et al. 2016) of the other terrestrial ones.

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Special section on Araceae

Introduction

Peter C. Boyce

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The five papers in the Araceae special section of this issue of Webbia are noteworthy for authorships which embrace Araceae research stretching back from the present day to the mid-1970s.

Michael Grayum, began work on the Araceae began during a16 months posting as a resident researcher at Finca La Selva, Costa Rica, between 1978–1980 when he became fascinated by one of the most diverse and taxonomically challenging plant families at the site. An informal checklist of La Selva aroids was published in 1982 (Grayum 1982). After leaving La Selva Mike enrolled as a graduate student University of Massachusetts (Amherst) undertaking a survey of Araceae pollen using scanning-electron microscopy, complemented by an extensive literature review and pioneering the use of cladistic techniques to work out a phylogenetic classification. The resulting 1984 Ph.D. dissertation (*Palynology and phylogeny of the Araceae*) suggested changes to the prevailing classification of family, most notably, the removal of the genus *Acorus* (Grayum 1987). The radical new phylogenetic classification was presented at the second international workshop on aroid systematics at Harvard Forest in 1984 and published by in 1990 (Grayum 1990) and followed by a comprehensive survey of pollen morphology (Grayum 1992). Between 1986 and 1990, while resident in Costa Rica, Grayum undertook botanical exploration in that country, as well as Mexico, Panama, Colombia, Ecuador, Jamaica, and Dominica, focusing on *Philodendron* subgen. *Pteromischum* with a view to produce a regional revision of that taxon which he had identified as being particularly intractable during residence at La Selva). The revision of *Philodendron* subgen. *Pteromischum* was published in 1996 (Grayum 1996). In 2003 based principally on field studies in Costa Rica over a 20-year period (1978–1998), the treatment of Araceae for the *Manual de Plantas de Costa Rica* (initiated in 1986) was published (Grayum 2003). Since 2003, Grayum has been one of the editors for *Manual* project, although continuing to undertake field word in Costa Rica and Panamá.

Alistair Hay has been working on the Araceae, particularly in the Malesian region, for more than forty years. He is now retired from the Royal

Botanic Gardens Sydney, but is currently working on a book on the classification, natural history, evolution and biogeography of the Araceae world-wide. Among numerous taxonomic papers are revisionary taxonomic accounts for the Lasioids (Hay 1988, 1992), Malesian *Alocasia* (Hay and Wise 1991; Hay 1998, 1999a), *Colocasia* (Hay 1996a), Potheae (Hay 1995; Boyce and Hay 2000), and Schismatoglottideae (Hay 1996b, Hay and Yuzammi 2000, Bogner and Hay 2000), *Homalomena* for New Guinea (Hay 1999b), and the Araceae for the Flora of Australia (Hay 2011). One of Alistair's primary interests is the reinterpretation of the reproductive structure (the spathe-and-spadix) of Araceae arguing that it does not fully align with the concepts either of flower or inflorescence, but rather has properties of both (Hay and Mabberley 1991; Mabberley and Hay 1994; Hay 2019). Four of the papers presented here utilize these reinterpreted terminologies.

Peter Boyce has been working on aroids since the early 1980s, initially focussing on the genera of the Mediterranean basin, producing monographs on *Arum* (Boyce 1996), and *Biarum* (Boyce 2008), and since 1987 the aroids of the tropical Asia, in particular SE Asia, concentrating especially on the extraordinarily rich flora of Borneo. Aside from co-authoring *The Genera of Araceae* (Mayo et al. 1997), and floristic accounts for China (Li et al. 2010) and Thailand (Boyce et al. 2012) the main outputs for tropical Asia concern the genera *Epipremnum* (Boyce 1998), *Rhaphidophora* (Boyce 1999, 2000a, 2000b, 2001a, 2001b), and *Pothos* (Boyce 2000c; Boyce and Hay 2000), and over 100 papers on the tribes Homalomenaeae and Schismatoglottideae, including a major reworking of generic boundaries (Low et al. 2018). In recent years he and his co-authors have incorporated Hay's reinterpretation of reproductive structures as standard.

Wong Sin Yeng began work on Araceae in 2005, publishing her first taxonomic paper the following year. Wong's taxonomic and phylogenetic outputs have concentrated primarily on the Homalomenaeae and Schismatoglottideae (Wong et al. 2010, 2013; Low et al. 2018), although her primary foci are the occurrence, morphological adaptations, categories, and evolution of rheophytism in the these tribes (Wong 2013; Boyce and Wong 2019), and the pollination biology for aroids (Hoe et al. 2016, 2018; Low et al. 2016; Chai and Wong 2019), *Tacca* (Chua et al. 2020), and *Scaphochlamys* (Ooi and Wong 2020).

Marco Cedeño-Fonseca recently obtained his Master's degree from the University of Costa Rica with a thesis on the taxonomy of Monstera (Araceae) in Costa Rica, and is now extending his work to a revision of the genus in Central America with Orlando O. Ortiz and Tom Croat. He has carried out field work not only in Costa Rica but also in Mexico, Panamá and Colombia, and has done work in the herbaria of the Missouri Botanical Garden and New York Botanical garden and other centres in Mexico and the USA where he has also lectured on Monstera taxonomy. Aside from his work on *Monstera* he has published papers on *Anthurium* (Cedeño-Fonseca et al 2019; Hay and Cedeño-Fonseca 2019) and *Dracontium* (Hay and Cedeño-Fonseca 2018).

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Studies on Potheae (Araceae) of Borneo II: *Pedicellarum* M.Hotta subsumed into *Pothos* L., and recognition of three new species

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Abstract. *Pedicellarum* is subsumed into *Pothos* as *Pothos paiei*. Four species, three taxonomically novel (*Pothos degenerans, ecclesiae* and *P. fractiflexus*) and one pre-existing (*Pothos oliganthus*) are discussed. The reproductive structures are reinterpreted and floral terminology used in this paper is in line with paving the way to interpreting the 'inflorescence' of *Pothos*, and indeed of all other aroids, as a unique array of structures that are neither flowers nor inflorescences as defined by current prevailing orthodoxy, but something of both.

Keywords: Borneo, Araceae, Potheae, *Pedicellarum*, *Pothos*.

INTRODUCTION

Pedicellarum paiei M.Hotta (Hotta 1976) is the sole described species of a genus of nomadic vines restricted to upper hill ridgetop kerangas in SW Sarawak. It was originally based on a single collection made close to the border between Sarawak and Kalimantan Barat in 1962, but later Nicolson (1984) drew attention to a previously overlooked second collection made 60 km further north about 35 years before. *Pedicellarum* has been considered unique amongst bisexual-floreted genera by possessing stipitate florets, with the top of the stipe swollen into a receptacle, an urceolate perigone of fused tepals, and (purportedly) introrse anther dehiscence. Grayum (1984: 634; 1992) remarked on a suite fertile and vegetative morphological similarities seemingly connecting *Pedicellarum* and *Pothos* species, and proposed a combination in *Pothos* although without effective publication (Grayum 1984: 634). Later, Grayum (1990: 670) revised his opinion and left the status of *Pedicellarum* unchanged. In fact, the earlier comparisons were based upon examination of material *(P.J.Martin & O.Ismawi S 36660)* mis-determined as *Pedicellarum* and then actually an undescribed species of *Pothos*.

Boyce and Hay (2001: 455) expanded on the similarities of *Pedicellarum* and *Pothos* species of the Goniurus supergroup (to which Hotta (1976) had also alluded relationship), noting the presence of a distinct receptacle, and fused tepals, and stating (as did Mayo et al. 1997) that anther dehiscence is latrorse, not introrse. Boyce & Hay also clarified the identity of the *P.J.Martin & O.Ismawi S 36660* collection referred to by Grayum (1990), describing it as a new species – *Pothos oliganthus* P.C.Boyce & A.Hay, and assigned an additional eight collections to *Pedicellarum*, extending the range of the genus south into Kalimantan Barat and north east to eastern Sabah.

While databasing specimens preparatory for the second author's Master's thesis it was necessary to reexamine the SAN duplicates of the two Sabah collections [*Fidilis Krispinus SAN 104271* and *Patrick Lassan SAN 107216*] assigned to *Pedicellarum paiei* by Boyce and Hay (2000), and study for the first time a third, later, collection [*Suzana S. SAN 154991*]. All three collections, although agreeing with *Pedicellarum paiei* in having stipitate florets on a characteristically zig-zagging axis, lack the characteristic conspicuous floral receptacle, and have the fused tepals forming a shallow saucer; additionally the leaf blades are proportionately narrower and thicker textured than in *P. paiei*, and more or less straight, lacking the characteristic narrowed falcate terminus, while the mid-rib is abaxially much more pronounced, and drying much paler than the surrounding tissues. It was obvious that these collections, gathered over 800 km to the north east of the Type of *Pedicellarum paiei*, represented an undescribed species. Thus alerted, we examined the other duplicates assigned to *Pedicellarum paiei*, starting with three Alison Church collections [*A.C. Church et al. 303*, *A.C. Church et al. 647*and *A.C. Church et al. 1014*] from Kalimantan Barat. While appearing an excellent match for *P. paiei* by having stipitate florets with a receptacle and chartaceous leaf blades with a conspicuously narrowed falcate terminus, detailed examination, however, revealed that although the perigone lobes are fused below, the tips are evidently free. Examination of two collections previously unseen (*P. Wilkie 94175* and *Tuke P9 1102*) from 75 km further south in Kalimantan Tengah confirmed the same morphologies. These five collections represented a third species distinct from both *Pedicellarum paiei* and from the Sabahan material.

Lastly, we turned attention to *F.H. Endert 2942* from central Kalimantan Timur and a previously unseen collection (*Bernard Lee Meng Hock S 45534*) from Belaga, Kapit, Sarawak. Both have overall similarity to the Sabah specimens in possessing straight coriaceous leaf blades with an abaxially pronounced mid-rib drying paler than the surrounding tissues. Examination of the blooms, however, revealed differences in the straight, not zig-zagging spadix axis, almost sessile florets with largely, but not wholly, fused tepals, and blooms all depauperate, each with just two or three florets. Moreover, the blooms are produced in dense fascicles and (presumably) sequentially.

These examinations of material previously associated with *Pedicellarum paiei* revealed that there are five species involved, with three – one from western Kalimantan, one from central Borneo, and one from Sabah – representing undescribed taxa. Furthermore, taken as a whole these species cover a full range of the combinations of the 'characters' used to define *Pedicellarum* and those of *Pothos* such that maintenance of *Pedicellarum* as genus separate from *Pothos* is no longer justifiable. We therefore propose that *Pedicellarum* be merged with *Pothos*, including transferal of *Pedicellarum paiei* to *Pothos*, and that the three taxonomically novel species discussed above be described in *Pothos*.

Some floral terminology used in this paper differs intentionally from those of previous papers on *Pothos* and is intended to pave the way to interpreting the 'inflorescence' of *Pothos*, and indeed of all other aroids, as a unique array of structures that are neither flowers nor inflorescences as defined by current prevailing orthodoxy, but something of both. For the background to this conceptual change see Hay (2019), Hay and Mabberley (1991), Mabberley and Hay (1994). The 'pedicellarums' described in this paper are perhaps particularly germane as they present some of the inflorescences or blooms, and flowers or florets of Araceae that most resemble, at least to first glance, racemose inflorescences of more or less standard pedicellate trimerous monocotyledonous flowers of text books. Nevertheless, this is an illusion.

First, the spadices in these species, where phenology is known, are protogynous as entities, which is the standard behaviour of Araceae. So, despite their strikingly distant positioning, the florets do not behave as individual flowers but act in concert in a protogynous spadix. Second, again a standard feature of Araceae, there are no bracts subtending the florets, in spite of the resemblance of the spadix to a raceme in these species. The use of the term 'pedicel' for the stalks of the individual florets is prejudiced towards the conventional interpretation of the bloom as an inflorescence, despite the absence of subtending bracts and the phenological behaviour of the florets being subordinate to that of the spadix. We therefore use the more neutral (in this context) term 'stipe' and the corresponding adjective 'stipitate', rather than describing the florets as 'pedicellate'.

Another interesting aspect of the morphology of the florets of this group of species concerns the perigon. That of the sessile florets of *Pothos oliganthus* consists, conventionally for *Pothos*, of six free tepals, whereas that of the stipitate florets of *Pothos paiei* is a truncate cupule set on what appears to be an enlarged receptacle. This cupule is conventionally interpreted as a perigone of connate tepals, though, since there are no apparent tepal lobes at all, it might also be suggested that the tepals have been *replaced* by this cupular outgrowth of the receptacle. [Sadly, there are no floral developmental studies of this species group, for which it is extremely hard to find suitable quantities of fresh material]. Were one to view floret variation here as a morphocline, of the species newly described in this paper, *Pothos degenerans*, with sessile florets and a proximally cupular but distally lobed perigone sits nearer to *P. oliganthus*; *Pothos ecclesiae*, with stipitate florets and like *P. degenerans* a proximally cupular and distally lobed perigone is somewhat nearer *P. paiei;* while *P. fractiflexus*, with stipitate florets and an entirely cupular (but very shallow) perigone is nearer still to *P. paiei.*

We cannot speculate on the ecological function of these strangely stipitate, cupular-perigonate florets. However, it is noteworthy that they occur in perhaps the most extreme leptocaul of all aroids, a family mostly with relatively to absolutely massive pachycaul construction (except Lemnoideae, of course). Perhaps extreme leptocauly can sometimes lead to structural decanalisation.

Infrageneric classifications referred to follow Boyce and Hay (2001: 454–455). Geological occurrences in this paper are verified with Tate (2001).

KEY TO *POTHOS PAIEI* AND ALLIES

1 a. Leaf blades with a conspicuous narrowed falcate terminus; florets stipitate **2**

b. Leaf blades straight; florets sessile or stipitate **3**

2 a. Tepals entirely connate into a cupular structure; receptacle conspicuous. SW Sarawak .... ***Pothos paiei***

b. Tepals basally connate, free from about half way from tip; receptacle inconspicuous. CW Kalimantan .... ***Pothos ecclesiae***

3 a. Florets stipitate, tepals connate into a shallow saucer. Sabah .... ***Pothos fractiflexus***

b. Florets sessile **4**

4 a. Spadix axis straight, not zig-zagging, with two or three florets; tepals largely but not wholly connate. C. Borneo .... ***Pothos degenerans***

b. Spadix zig-zagging, with up to seven florets; tepals free. SW Sarawak .... ***Pothos oliganthus***

Pothos L., Sp. Pl. 968. 1753. Schott, Aroideae 21–25, t.31–56 (1856–1857) & Gen. Aroid. 95 (1858) & Prodr. Syst. Aroid. 558–575 (1860); Engl. in Engl., Pflanzenr. 21 (IV.23B): 21–44 (1905); Mayo et al., Genera of Araceae 98–99, pl.5, 108, a. (1997) [— *Tapanava* Adanson, Fam. 2: 470 (1763), nom. superfl.] — Type: *Pothos scandens* L.

Goniurus Presl, Epimel. Bot. 244 (1851, '1849'). — Type: *Goniurus luzonensis ca* Presl [= *Pothos luzonensis* (C. Presl) Schott].

[*Potha* O. Kuntze, Rev. Gen. 2: 742 (1891), *orth. var.*].

Pedicellarum M. Hotta, Acta Phytotax. Geobot. 27(3–4): 61 (1976); Nicolson, Aroideana 7(2): 56–57 (1984); Mayo et al., Genera of Araceae 100, pl.6, pl.108B (1997); Boyce & Hay, Telopea 9(3): 254–258, Fig. 50 (2001), ***syn. nov.*** — Type: *Pedicellarum paiei* M. Hotta.

Pothos degenerans S.Y.Wong, P.C.Boyce & A.Hay, **sp. nov.**

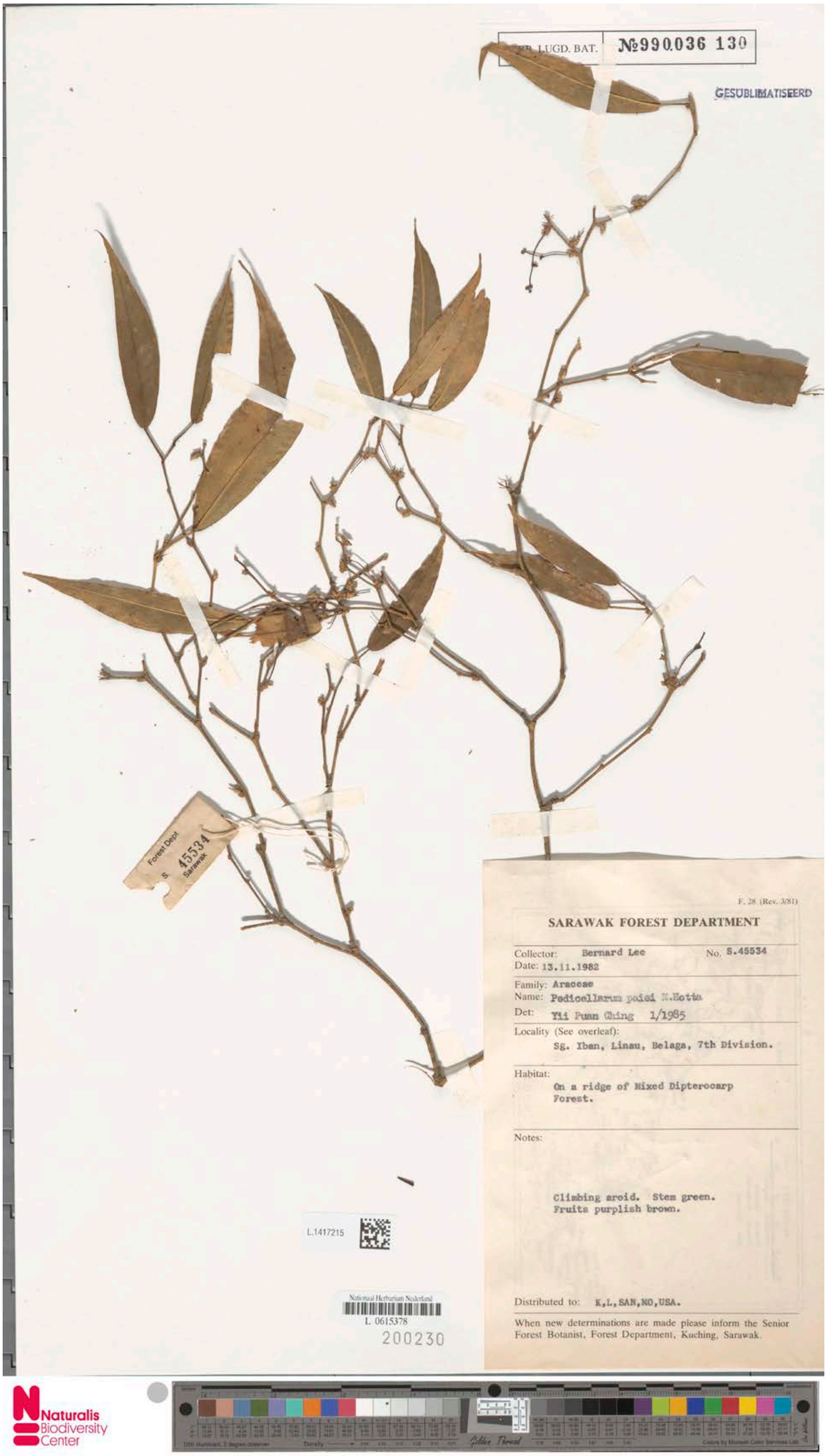
Type: Malaysia. Sarawak, Kapit [7th Division], Belaga, Linau, Sungai Iban, 18 Nov 1989, *Bernard Lee Meng Hock S 45534* (holotype SAR!; isotypes K!, L!, SAN!, MO, US!) (Figure 1).

Diagnosis

Pothos degenerans is most similar to *Pothos fractiflexus* by the straight coriaceous leaf blades with an abaxially pronounced mid-rib drying paler than the surrounding tissues. However, *Pothos degenerans* has up to 3 florets per spadix (vs 7 or more in *P. fractiflexus*), an almost straight or only very weakly (not strongly) zig-zagging spadix axis, sessile (vs stipitate) florets with a receptacle of partially (not wholly) fused tepals.

Description

Probably heterophyllous, root-climbing nomadic leptocaul vines. Adult shoot system not completely known



F. 28 (Rev. 3/81)

SARAWAK FOREST DEPARTMENT

Collector: Bernard Lee No. S.45534
Date: 13.11.1982

Family: Araceae
Name: Pedicellarum paiei M.Hotta
Det: Yii Puan Ching 1/1985

Locality (See overleaf):
Sg. Iban, Linau, Belaga, 7th Division.

Habitat:
On a ridge of Mixed Dipterocarp Forest.

Notes:
Climbing aroid. Stem green.
Fruits purplish brown.

Distributed to: K,L,SAN,NO,USA.

When new determinations are made please inform the Senior Forest Botanist, Forest Department, Kuching, Sarawak.

Figure 1. *Pothos degenerans – Bernard Lee Meng Hock S 45534*. Isotype [L].

but, in any case, differentiated into non-flowering orthotropic adherent stems, free lateral fertile stems, and much abbreviated cataphyll-encased (foliage-) leafless flowering shoots arising from below the petiole insertion; eocaul, seedling, and flagellate foraging shoots unknown. Leaves stiffly but thinly coriaceous, drying medium brown, abaxially somewhat paler with the prominent mid-rib markedly paler; petiole 1–2 × 0.1–0.2 cm, slender, very narrowly canaliculate, apex geniculate, sheath indistinct; blade 5–11 × 1.5–3 cm, narrowly elliptic, apex acute, apiculate, base subacute to obtuse; primary lateral veins arising at 60–70°, two intramarginal veins per side, 2–3 mm from blade margin, arising from just above base of the midrib, remaining ± parallel to margin, terminating at the tip of the blade. Blooms in fascicles of up to ten per flowering shoot; peduncle 6–8 × 1 mm, very slender, straight, the bloom spreading, purplish brown. Spathe 4 × 4 mm, ovate, base rounded, amplexicaul on peduncle, cucullate-concave, apex briefly acuminate, purplish brown. Spadix stipitate; stipe 10 × ca 0.9 mm, terete, amounting to about ¾ of entire spadix; fertile portion 10 × 1.5 mm, slender cylindric, almost straight, purplish brown. Florets up to 3 per spadix, ca 2 mm diam., loosely clustered, sessile; tepals basally fused apically free; stamens six, free; filaments broader than the anthers; pistil oblong-cylindric, truncate, purplish brown. Infructescence, fruits and seeds unknown.

Etymology

From Latin *degenerans*, reduced, in allusion to the blooms, the smallest yet recorded for the genus, each with at most three florets.

Distribution

Central Borneo, known from two localities approximately 300 km apart.

Ecology

Lowland forested ridges and riverine forest, to about 200 m asl. The Kapit collection is from Eocene sedimentaries, the Kalimantan one from Cretaceous-Jurassic deepwater sediments.

Notes

The remarkably slender and diminutive blooms of *Pothos degenerans* are both easily overlooked and readily detached from specimens. Each flowering node has numerous denuded pedicels indicating blooms produced in fascicles, but it is not possible from the available specimens to determine if the blooms mature in a sequential series (as in all known *Pothos* producing fascicles of blooms), or if all the blooms in a fascicle reach anthesis simultaneously. The absence of any fruiting seems to favour the second scenario except that the large number of missing blooms indicated by the barren pedicels might have taken with them any developing fruits – favouring the first scenario.

Other specimen examined

BORNEO: Indonesia. Kalimantan Tengah, Kutai Barat [West Koetai], No. 28, near Long Liah Leng, 200 m, 28 Aug 1925, *F.H. Endert 2942* (AAH, BO, K, L).

Pothos ecclesiae P.C.Boyce, S.Y.Wong & A.Hay, **sp. nov.**

Type: Indonesia, Kalimantan Barat, Sintang, HPH km 69-73, west of camp off main (new) logging road, cutting black and surrounding environs, 0°51'53.6"S 112°13'29.9"E, 150 m, 19 April 1994, *A.C. Church et al. 1014* (holotype NY!; isotypes AAH!, BO, K!) (Figures 2 and 3).

Diagnosis

Pothos ecclesiae is most easily confounded with *Pothos paiei* in having a conspicuous receptacle, stipitate florets, and chartaceous leaf blades with a conspicuously narrowed falcate terminus. However, the free perigone lobes of *Pothos ecclesiae* are immediately diagnostic. The two species are also ecologically dissimilar, with *P. ecclesiae* occurring in lowland dipterocarp-dominated forest on red clay soils whereas *P. paiei* occurs on upper hill kerangas ridges.

Description

Probably heterophyllous, root-climbing nomadic leptocaul vines. Adult shoot system not completely known, from available material differentiated into non-flowering orthotropic adherent stems, free lateral fertile stems, and much abbreviated cataphyll-encased (foliage-) leafless flowering shoots arising from below the petiole insertion; eocaul, seedling, and flagellate foraging shoots unknown. Leaves chartaceous, drying dull pale brown; petiole 1–3 × 0.1–0.2 cm, slender, very narrowly canaliculate, apex geniculate, sheath indistinct, no sign of it clasping the stem in material available; blade 5–17 × 1.5–5 cm, elliptic or ovate-elliptic, with one side unequal to the other, apex long-acuminate, markedly falcate, apiculate, base subacute to obtuse; primary lateral veins arising at 60–70°, 2 intramarginal veins per side, 2–15 mm from blade margin, arising from just above base of the midrib, remaining ± parallel to margin, terminating at the tip of the blade. Blooms solitary to rarely paired;

Plants of Indonesia

Araceae
Pedicellarum paiei

Determined by:

Locality:
Borneo. C. Kalimantan. Sintang. HPH Km 69-73; West of camp off main (new) logging road, cutting block and surrounding environs.

Lat.:	0 °	51 '	53.6 "	S
Long.:	112 °	13 '	29.9 "	E

Habitat **Alt.** 150 **m**
Mixed Dipterocarp forest, associates: Shorea, Vatica, Horsfieldia. Newly disturbed forest. Red clay soil.

Morphology:
Climber, c .5 m long. Inflorescence yellow, 5 cm long. Flower with green ring around apex. Fruit bright red, oblong, 2.5 cm.

Local name:

Notes: Slide: Fl & Fr 1:4, 1:3, 1:1.7

Church, A.C., Mahyar, U.W. ,Indah, Ismail, and Hamzah
1014
Tuesday, April 19, 1994
HERBARIUM BOGORIENSE
HARVARD UNIVERSITY HERBARIA

Figure 2. *Pothos ecclesiae – A.C.Church et al. 1014*. Holotype [NY].

Figure 3. *Pothos ecclesiae – A.C.Church et al. 1014*. Isotype [L].

peduncle 6–8 × ca 0.1 mm, very slender, straight, the bloom held erect to spreading, greenish yellow. Spathe 4–6 × ca 4 mm, ovate, base rounded, amplexicaule on peduncle, cucullate-concave, apex somewhat acuminate, yellow. Spadix stipitate; stipe 10–11 × ca 0.9 mm, terete; fertile portion 2–3 × ca 0.15 cm, slender cylindric, prominently zig-zagging at each floret insertion, yellow. Florets five to eight per spadix, ca 2 mm diam., widely scattered, stipitate, with a receptacle; tepals six, fused to about half way; stamens six, free; filaments slightly broader than the anthers; pistil oblong-pyriform, truncate, yellow. Infructescence with rather few berries; fruit 6–13 × 4–6 mm, elongate oblong-ellipsoid with a rounded apex, ripening glossy scarlet; seeds elongate-ellipsoid, 4–6 × 3–4 mm.

Eponymy

From Latin, *ecclesiae*, literally 'of the church', devised to commemorate Alison C. Church, collector of the Type material.

Distribution

SW Borneo.

Ecology

Lowland mixed old secondary dipterocarp forest on red clay soils, 150–315 m asl. The three Alison Church collections are from the pre-Carbonifeous Pinoh metamorphics of the Schwaner Range while *P. Wilkie 94175* and *Tuke P9 1002* are from Lower Cretaceous granites to the south.

Notes

Fig. 50 in Boyce & Hay 2001: 557, depicting *Pedicellarum paiei* and cited as being a drawing of *Church et al. 1014*, was mislabelled. The plate was prepared from the Type material of *Pedicellarum paiei*. The notes accompanying *A.C. Church et al. 303* state the fruit to be edible and sweet.

Other specimens examined

BORNEO**:** Kalimantan: Kalimantan Barat. Sintang, Bk. Baka National park, along bank of Sungai Ella, 600 m east of camp, 0°38'S 112°17'E, 315 m, 22 October 1993, *A.C. Church et al. 303* (AAH, BO, K, L); Bukit Baka National Park, 200 m from logging road between km 39 and km 40, environs bordering national park and SBK, 0°37'S 112°15'E, 310 m, 9 Nov 1993, *A.C. Church et al. 647* (AAH, BO, L). Kalimantan Tengah. Kotawaringin Timur, Plot 11, km 92 from Sangai (Sungai Mentaya), 1 29'S 112 31'E', 50 m, 14 Apr 1994, *P. Wilkie 94175* (E, L); Plot 9, km 92 from Sangai (Sungai Mentaya), 1 29'S 112 31'E', 50 m, 1994, *Tuke P9 1002* (AAH, E, L).

Pothos fractiflexus J.Joling, Pereira & A.Damit, **sp. nov.**

Type: Malaysia, Sabah. Interior Division, Nabawan, Syt. Benawood, Sg. Maadun, 15 May 1987, *Fidilis Krispinus SAN 104271* (holotype SAN!) (Figures 4 and 5).

Diagnosis

Pothos fractiflexus is similar to *Pothos paiei* in having stipitate florets on a characteristically zig-zagging spadix axis but differs in the fused tepals forming a shallow saucer (vs florets with an enlarged floral receptacle and tepals fused into a cupular structure), leaf blades proportionately narrower and thicker textured, and more or less straight (vs leaf blades chartaceous with a characteristic narrowed falcate terminus), and with the midrib abaxially much more pronounced, and drying much paler than the surrounding tissues.

Description

Probably heterophyllous, root-climbing nomadic leptocaul vines. Adult shoot system not completely known, at least differentiated into non-flowering orthotropic adherent stems, free lateral fertile stems, and much abbreviated cataphyll-encased (foliage-) leafless flowering shoots arising from below the petiole insertion; eocaul, seedling, and flagellate foraging shoots unknown. Leaves stiffly coriaceous, drying medium brown, abaxially somewhat paler with the prominent mid-rib markedly paler; petiole 1–2 × 0.1–0.2 cm, slender, very narrowly canaliculate, apex geniculate, sheath very indistinct; blade 5–11 × 1.5–3 cm, narrowly elliptic, apex acute, apiculate, base subacute to obtuse; primary lateral veins arising at 60–70°, two intramarginal veins per side, 2–3 mm from blade margin, arising from just above base of the midrib, remaining ± parallel to margin, terminating at the tip of the blade. Blooms solitary or paired; peduncle 6–8 × 1 mm, very slender, straight, the bloom spreading, yellowish. Spathe 4 × 4 mm, ovate, base rounded, amplexicaule on peduncle, cucullate-concave, apex briefly acuminate, yellowish. Spadix stipitate; stipe 10 × ca 0.9 mm, terete; fertile portion 10 × 1.5 mm, slender cylindric, strongly zig-zagging, yellowish. Florets up to 7 per spadix, ca 2 mm diam., loosely clustered, sessile; tepals wholly? connate into a shallow saucer; stamens 6, free; filaments broader than the anthers; pistil oblong-cylindric, truncate, yellowish. Infructescence with rather few berries; fruit 6–13 × 4–6 mm, elongate oblong-ellipsoid with a rounded apex, ripening glossy scarlet; seeds

To be returned to:—
Herbarium, Forest Department,
SANDAKAN, Sabah,
E. Malaysia.

104271

SAN 104271

SAN. № 104271

FLORA OF SABAH
HERBARIUM OF THE FOREST DEPARTMENT SANDAKAN

No. SAN 104271
Family Araceae
Botanical Name ~~Pedicellarum~~ Pothos sp.
Det.
Vernacular
Dialect
Locality (see reverse for map) Syt.Benawood, logged area, sg.Ma
District Nabawan
Alt. m.a.s.l.
Collector Fidilis krispinus
Date 15.5.87
Habitat Hillsides
Notes :
Fruits yellowish green, parasite climber about 1 m long.

Duplicates to : K/L/SAR/KEP/SING/BO/PNH/AA/OX/

Herbaria receiving duplicates are requested to communicate new identifications to the Forest Botanist, ~~Forest Research~~ Centre, Sandakan, Sabah.

SFC 1001H

INDEXED

ARACEAE REINDEXED
Pedicellarum paiei M. Hotta
Det. P.C. Boyce, August 2001
Royal Botanic Gardens, Kew (K)

83000

27 OCT 1987

Figure 4. *Pothos fractiflexus – Fidilis Krispinus SAN 104271*. Isotype [SAN].

elongate-ellipsoid, 4–6 × 3–4 mm.

Etymology

From *fractiflex* – zig-zagging – used to describe the spadix axis.

Distribution

East Sabah.

Ecology

Forested hillsides on Neogene or Quaternary sediments between 300 and 500 m asl.

Notes

In general appearance very close to *Pothos degenerans*, but readily differentiated by stipitate florets and shallow saucer-like perigone.

Other specimens examined

BORNEO: Sabah: Sandakan Division. Ulu Sg. Pinangah, 17 Oct 1984, *Patrick Lassan SAN 107216* (L, K, SAN); Interior Division. Sapulut, Nurod-Urod F.R., 4°35'10"N 116°54'27"E, 582 m asl, 14 Jun 2012, *Suzana S. SAN 154991* (SAN).

Figure 5. *Pothos fractiflexus – Fidilis Krispinus SAN 104271*. Isotype [SAN] – detail of the blooms.

Pothos oliganthus P.C.Boyce & A.Hay, Telopea 9(3): 552. 2001

Type: Malaysia, Sarawak, Sri Aman Division [2nd Div.], 85th mile, Ulu Sg. Silantek Kiri, path from Gunung Silantek, 300 m, 26 Aug 1980, *Ilias Paei S 42566* (holotype K!; isotypes AAH!, L!, MO!, SAN!, SAR!). (Figure 6).

Description

Probably heterophyllous, root-climbing nomadic leptocaul vines. Adult shoot system not completely known, at least differentiated into non-flowering orthotropic adherent stems, free lateral fertile stems, and much abbreviated cataphyll-encased (foliage-) leafless flowering shoots arising from below the petiole insertion; eocaul, seedling, and flagellate foraging shoots unknown. Leaves somewhat coriaceous, drying greenish brown; petiole 0.4–3 × 0.1–0.12 cm, slender, very narrow-canaliculate, apex weakly geniculate, sheath distinct, prominent, erect, apically ligulate in young growth, ligule later disintegrating; blade 6–21 × 1–4.5 cm, very narrowly to narrowly elliptic, oblique, weakly falcate, apex long-acuminate, apiculate, apicule later deciduous, base obtuse; primary lateral veins arising at 60–70°, two intramarginal veins per side, 2–8 mm from blade margin, arising from just above base of the midrib, remaining ± parallel to margin, terminating at the tip of the blade. Bloom solitary, rarely several at different stages on a reiterating flowering shoot; peduncle 0.3–1.3 × 0.05–0.1 cm, very slender, pale green. Spathe ca 3 × 2 mm, oblong-ovate, cucullate, base rounded and amplexicaule on peduncle, apex acuminate, white. Spadix stipitate; stipe 1–7 mm long, terete; fertile portion 0.3–0.5 cm, very slender-cylindric, white. Florets usually three, up to six per spadix, sessile, ca 1.5 mm diam., slightly scattered, with six free tepals and six stamens. Pistil squat oblong cylindric, truncate. Infructescence with few fruits; fruit (immature) 3–5 × 2–3 mm, obclavate ellipsoid; seeds not observed.

Distribution

Endemic to SW Sarawak.

Habitat

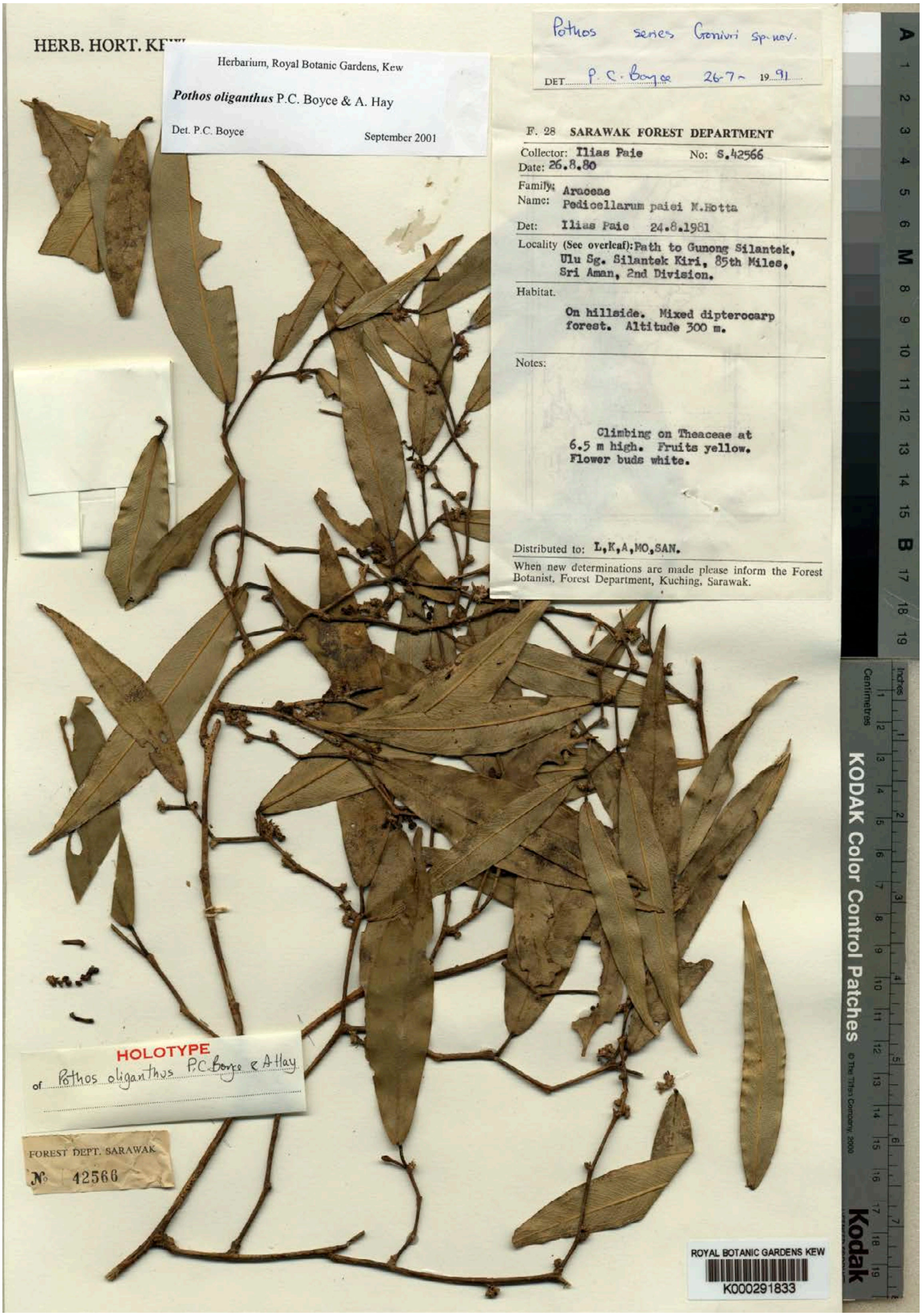
Mixed lowland to hill dipterocarp forest on slopes and ridges of Upper Cretaceous granite-derived yellow sandy clays, 300–540 m altitude.

Notes

Despite being earlier confounded with *Pothos* [*Pedicellarum*] *paiei*, *P. oliganthus* is readily differentiated by the stiffly leathery narrowly elliptic leaf blades, sessile florets, and free tepals. In overall appearance the narrow stiff leaf blades of *Pothos oliganthus* make it reminiscent of *P. degenerans* and *P. fractiflexus* and like *P. degenerans*, *P. oliganthus* has blooms with very few sessile florets.

Other specimens examined

BORNEO: Sarawak: Samarahan Division [1st/2nd Div. Boundary], [Simunjan], Gunung Buri, 75th mile, 540 m,



HERB. HORT. KEW

Herbarium, Royal Botanic Gardens, Kew

Pothos oliganthus P.C. Boyce & A. Hay

Det. P.C. Boyce September 2001

Pothos series Goniuri sp. nov.

DET P. C. Boyce 26-7- 19 91

F. 28 SARAWAK FOREST DEPARTMENT

Collector: Ilias Paie No: S.42566

Date: 26.8.80

Family: Araceae

Name: Pedicellarum paiei M.Hotta

Det: Ilias Paie 24.8.1981

Locality (See overleaf): Path to Gunong Silantek, Ulu Sg. Silantek Kiri, 85th Miles, Sri Aman, 2nd Division.

Habitat. On hillside. Mixed dipterocarp forest. Altitude 300 m.

Notes: Climbing on Theaceae at 6.5 m high. Fruits yellow. Flower buds white.

Distributed to: L,K,A,MO,SAN.

When new determinations are made please inform the Forest Botanist, Forest Department, Kuching, Sarawak.

HOLOTYPE

of Pothos oliganthus P.C. Boyce & A Hay

FOREST DEPT. SARAWAK

No 42566

ROYAL BOTANIC GARDENS KEW

K000291833

Figure 6. *Pothos oliganthus* – *Ilias Paie S 42566*. Holotype [K].

12 Sep 1975, *P.J. Martin & O. Ismawi S 36660* (K, KEP, L, MO, SAR, US); Samarahan Division [1st Division], [Simunjan], Gunung [Bukit] Buri, 440 m, 25 May 1981, *Ilias Paie S 42082* (K, L, SAN, SAR, US).

Pothos paiei (M.Hotta) S.Y.Wong, A.Hay & P.C.Boyce, **comb. nov.**

Basionym: *Pedicellarum paiei* M. Hotta, Acta Phytotax. Geobot. 27(3–4): 61–65 (1976); Nicolson, Aroideana 7(2): 56–57 (1984); Mayo et al., Genera of Araceae 100, pl. 6 &108B (1997); Boyce and Hay, Telopea 9(3): 254–258, Fig. 50 (2001).

Type: Malaysia, Sarawak, Serian Division, [9th Div.], Gunung Penrissen, 914 m., 3 May 1962, *Ilias Paie S 16354* (holotype KYO!; isotypes K!, L!, SING!). (Figures 7 and 8).

Description

Heterophyllous, root-climbing nomadic leptocaul vines. Adult shoot system differentiated into non-flowering orthotropic adherent stems, free lateral fertile stems, and much abbreviated cataphyll-encased (foliage-) leafless flowering shoots arising from below the petiole insertion; eocaul and flagellate foraging stems resembling slender green wire, furnished with tiny distantly-spaced acute bracts; seedling and newly climbing foraging stems shingling with leaf blades ovate with short rounded basal lobes separated by a very narrow sinus and a briefly cuspidate tip, stems somewhat flattened and longitudinally sulcate on the narrow sides. Leaves chartaceous, rather bright semi-glossy mid-green, scarcely paler abaxially; petiole 1–7 × 0.1–0.3 cm, slender, very narrowly canaliculate, apex geniculate, sheathing until just below apical geniculum, sheath wings very narrow, initially clasping the stems, later spreading, extended into a brief narrow blunt ligule; blade 5–16 × 1.5–5 cm, elliptic or ovate-elliptic, usually with one side unequal to the other, apex long-acuminate, markedly falcate, apiculate, apicule later deciduous, base subacute to obtuse; primary lateral veins arising at 60–70°, two intramarginal veins per side, 2–6 mm from blade margin, arising from just above base of the midrib, remaining ± parallel to margin, terminating at the tip of the blade. Blooms solitary to rarely paired; peduncle 6–8 × ca 0.1 mm, very slender, straight, the bloom held erect to spreading, greenish yellow. Spathe 4–6 × ca 4 mm, ovate, base rounded, amplexicaul on peduncle, somewhat cucullate-concave, apex briefly acuminate, greenish yellow. Spadix stipitate; stipe 3–4 × ca 0.9 mm, terete; fertile portion 2–3.5 × ca 0.15 cm, slender cylindric, prominently zig-zagging at each floret insertion, greenish yellow. Florets five to eleven per spadix, ca 2 mm diam., widely scattered, briefly stipitate, arranged in two rather irregular rows along the spadix; receptacle prominent; tepals 6, fused into an urceolate cup; stamens six, free; filaments broader than the anthers. Infructescence with few berries; fruit 6–13 × 4–6 mm, elongate oblong-ellipsoid with a truncate apex, ripening glossy scarlet; seeds elongate-ellipsoid, 4–6 × 3–4 mm.

Distribution

SW Sarawak.

Habitat

Primary to disturbed secondary upper hill ridge kerangas forest between 600–950 m altitude.

Other specimens examined

BORNEO**:** Sarawak: Kuching Division. [1st Div.], proposed Matang National Park, Ulu Sg. Rayu, 27 Apr 1987, *Bernard Lee Meng Hock S 54080* (K, KEP, L, SAN, SAR, US); Mount Matang, 700 m asl, 1927–1928, *'Native collector' 5178 Collected through the Sarawak Museum for the California Botanic Garden* (NY).

ACKNOWLEDGEMENTS

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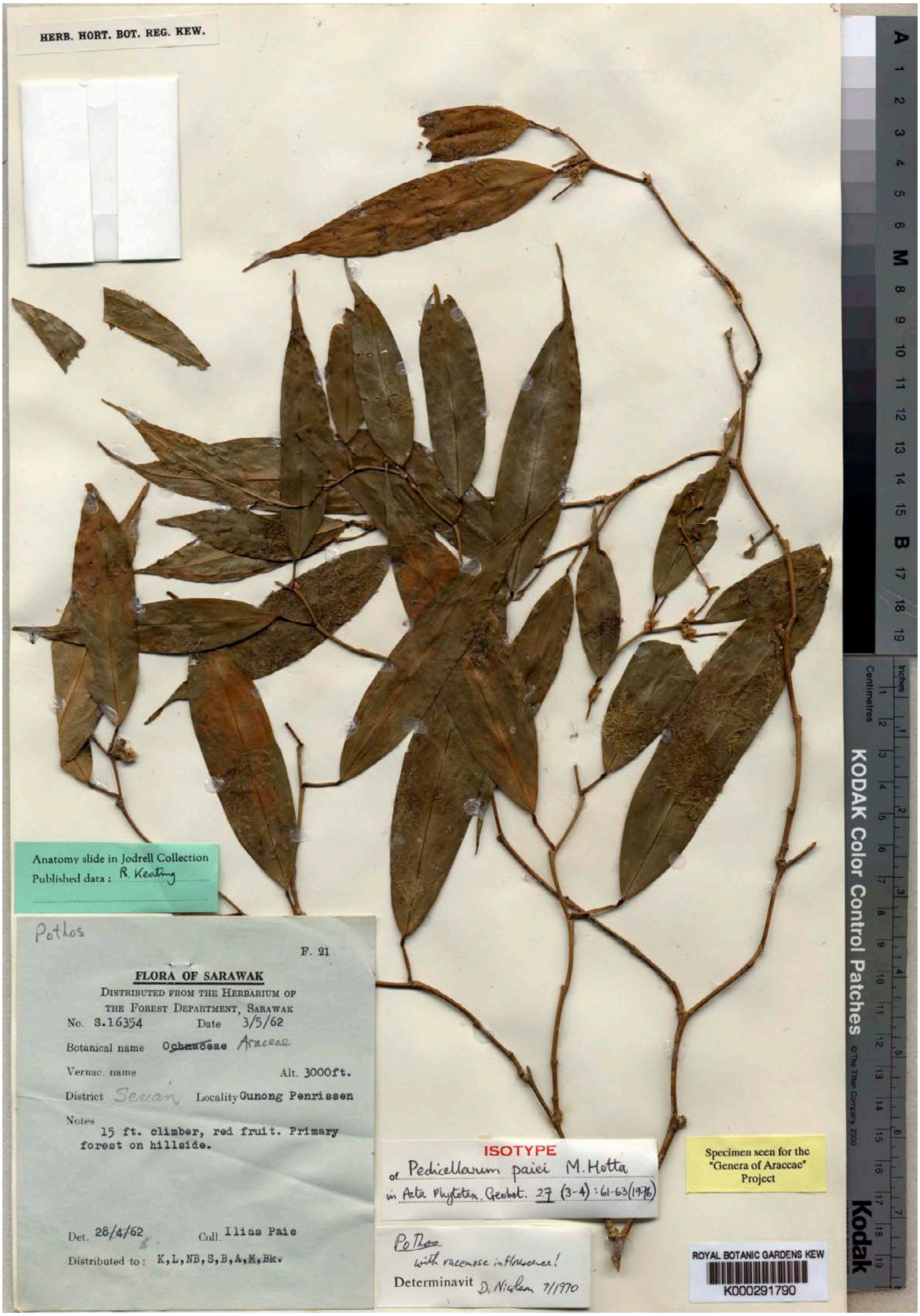

Figure 7. *Pothos paiei – Ilias Paie S 16354*. Holotype [K].

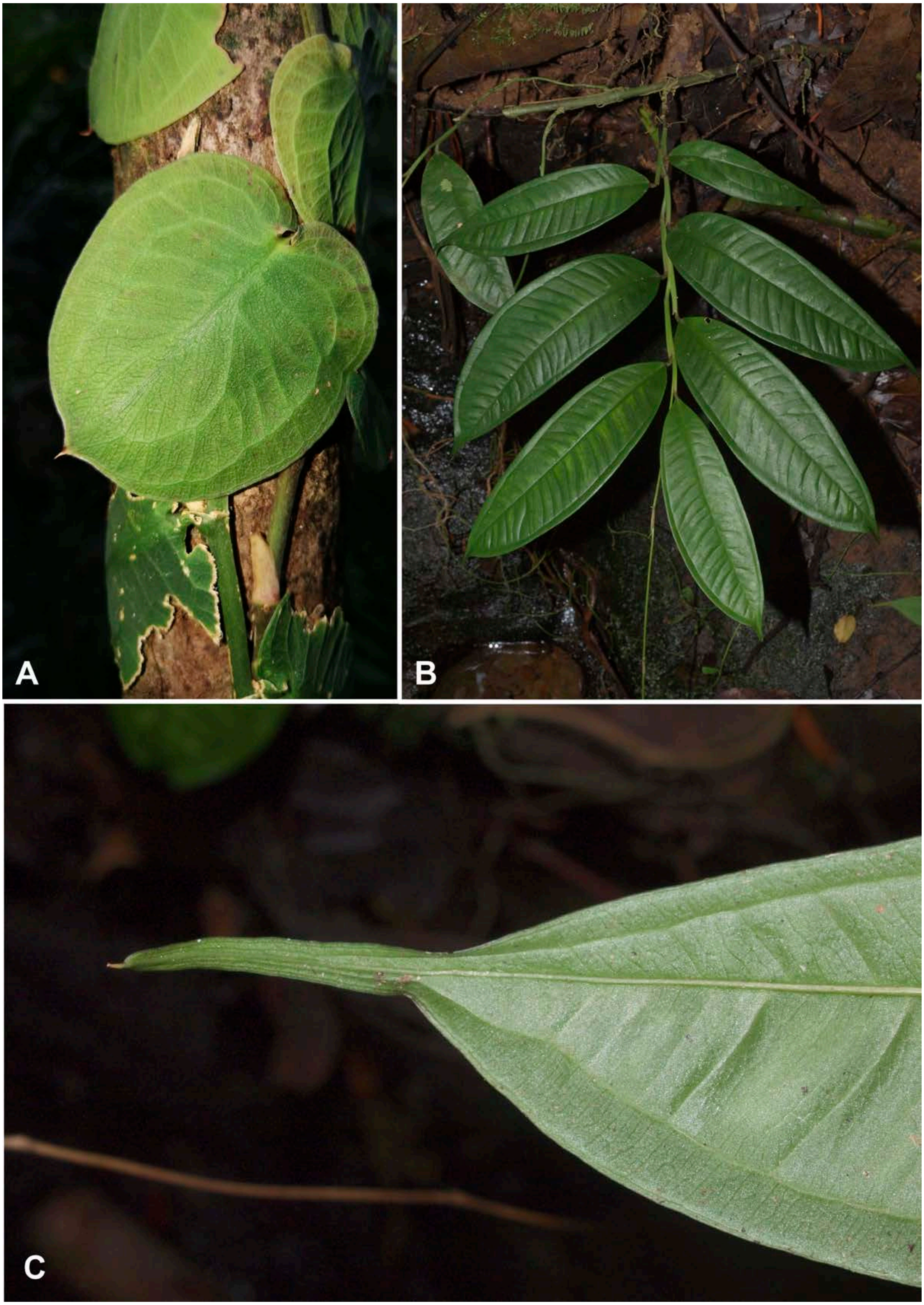

Figure 8. *Pothos paiei* in habitat in the general vicinity of the type location. All from *AR-4974*.

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Studies on Schismatoglottideae (Araceae) of Borneo LXIX: *Schismatoglottis imbakensis*, a new species of the Patentinervia Complex from ultramafic rocks, Sabah

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[3] *Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak 94300 Kota Samarahan, Sarawak, Malaysia*
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*Corresponding author. E-mail: k_saibeh@ums.edu.my

Abstract. *Schismatoglottis imbakensis* is described as a new species of the *Schismatoglottis* Patentinervia Clade from forested ultramafic rocks, and compared with *S. retinervia* Furtado, the only the species for the clade yet described from Sabah.

Keywords: *Schismatoglottis*, Patentinervia clade, Sabah, Borneo.

INTRODUCTION

The *Schismatoglottis* Patentinervia Clade is entirely Bornean (Wong et. al., 2017, 2019), comprising small mesophytic herbs with highly distinctive lanceolate to oblong-elliptic to narrowly obovate leaf blades lacking posterior lobes, and with ladder-like rather closely spaced numerous primary lateral veins diverging from the mid-rib at about 90°. At present the clade comprises 11 described species, 8 of which have been described in the past three years (Boyce 2017; Wong et al. 2017, 2018, 2019). Until now, only one species of the Patentinervia Clade has been recorded from Sabah, *Schismatoglottis retinervia* Furtado (1935), restricted to the vicinity of Kinabalu between 1000 and 1600 m asl on granite.

During a Borneo Geographic Scientific Expedition organised by Universiti Malaysia Sabah (UMS) and the Sabah Foundation to the Sungai Kangkawat, Imbak Canyon Conservation Area (ICCA), the first author encountered a small colony of a highly distinctive *Schismatoglottis* with venation suggesting a species of the Patentinervia Clade. At the time of discovery the plants were sterile although their distinctive morphology and occurrence on ultrabasic rocks let us to suspect they represented an undescribed species. Subsequently the plant flowered in the living collection of UMS revealing the plant to be a taxonomic novelty of the Patentinervia Clade, and furthermore the forst species of the clade recorded from ultramafic rocks. It is described here as *Schismatoglottis imbakensis*.

The Imbak Canyon Conservation Area is located immediately to the north of Maliau Basin Conservation Area in central Sabah. The canyon of Cretacoues to Paleogene deep water sediments with ultramafic outcrops encompasses a range of lowland to hill forest habitats within a 10 km long valley (at about 250 m asl.), hemmed in on three sides by sandstone ridges up to 1000 m asl. (Oldfield 2014). The Kangkawat Research Station is located at the eastern part of the canyon near to the Sungai Kangkawat river. And close by Cretaceous outcroppings of ultramafic Harzburgite and Serpentinite.

Dimensions in the descriptions are from fertile (i.e., mature) plants. Seedlings have overall smaller measurements. Geological occurrences in this paper are verified with Tate (2001).

Schismatoglottis imbakensis Kartini, S. Y. Wong & P. C. Boyce, **sp. nov.**

Type: Malaysian Borneo. Sabah. East Coast Division, Telupid, Imbak Canyon Conservation Area, Sungai Kangkawat, 1 Oct 2018, 5°5'4.62"N 117°3'20.10"E, ca 260 m asl, (holotype BORH 2705 + spirit). (Figures 1 and 3A).

Diagnosis

Schismatoglottis imbakensis is distinguished from *S. retinervia*, the only other species of the Patentinervia clade occurring in Sabah, by the plant glabrous (vs petioles and abaxial midribs puberulous), by the naked sterile interstice of the spadix equalling the pistillate floret zone (vs naked sterile interstice hardly developed), by the deep green pistils with the stigma about half the width of the ovary (vas pistils dirty pale green with the stigma almost equalling the ovary width), by the staminate florets somewhat laxly arranged and the stamens readily discernible (vs staminate florets very densely packed and individual stamens scarcely distinguishable). *Schismatoglottis imbakensis* is distinguished from *S. pichinensis* and *S. puncakborneensis*, the other two Patentinervia clade species with a long naked sterile interstice, by large rhomboidal cream interpistillar staminodes (vs interpistillar staminodes lorate or if rhomboidal then small and white), the large, laxly arranged stamens (vs small and congensted), and sharply pointed (vs blunt) spadix appendix.

Description

Small, colony-forming mesophytic herb to ca 10 cm tall. Stem epigeal, erect to sprawling, rather elongate, to c. 50 cm long, c. 0.5 cm diam., decumbent portions tending to root along their length, modules pleionanthic, internodes 0.2–1 cm long, green. Leaves many together along distal parts of stem and tending to become clustered at apex; petiole 3–4 cm long, D-shaped in cross-section, sheathing in lower 1/2-2/3, pale green, glabrous; petiolar sheath wings fully attached to petiole, rather wide and tending to be flat, membranous, long-persistent; leaf blades glossy metallic dark green adaxially, much paler abaxially, oblong-elliptic, 4–6 cm long × 1.5–2 cm wide, base cuneate, apex blunt with a brief tubular mucro ca 0.5 mm long; midrib abaxially prominent, adaxially slightly impressed into blade; primary lateral veins about 9 on each side, mostly alternating with barely lesser interprimaries, diverging at 80–90° from midrib, then gradually and evenly curving up to meet margin, abaxially rather prominent; interprimaries almost indistinguishable from primaries, occurring more or less equally between them; secondary venation mostly arising from midrib, occasionally from base of primary veins; tertiary venation abaxially forming a faint tessellate reticulum. Inflorescence solitary; peduncle to c. 1cm long, more often peduncle and part of lower spathe obscured by leaf bases, pale green. Spathe 3–3.5 cm long; lower spathe c. 1.5 cm long, ovoid, differentiated from limb by a marked constriction, semi glossy pale green; spathe limb ovate, c. 1.5-2 cm long, mucronate for 0.5-1 mm, opening slightly at pistillate anthesis, white at anthesis, later darkening and rotting-deciduous. Spadix sub-equalling spathe, sessile; pistillate floret zone c. 7 mm long, conoid; pistils crowded, subglobose, 1 mm diam., dark green; stigma sessile, button-like, subequalling diameter of ovary, pale green, conspicuously papillate at anthesis; interpistillar staminodes confined to a ring at base of pistillate zone, rhomboid, glossy cream, ca 1 mm across; sterile interstice attenuate, naked ca 3 mm long, pale green; staminate zone rather stoutly obconoid, ca 8 mm long, 2.5 mm diam. at base, 6 mm diam. distally; stamens rather lax, dumbbell-shaped, truncate with connective flat between thecae; pores joined across the anther by a narrow deep slit, each with a heavily thickened rim, dull white; appendix wider than the widest part of the with staminate flower zone, stoutly conic, blunt, ca 1.5 cm long; appendix staminodes composed of irregularly rhomboidal to polygonal-shaped, truncate staminodes c. 1 mm diam., creamy white. Fruiting spathe urceolate, ca 1 cm long, mid-green.

Figure 1. *Schismatoglottis imbakensis* (A) Plants in habitat. (B) Inflorescence at pistillate anthesis. The spathe limb slightly open. (C) Spadix at pistillate anthesis with the spathe artificially remove (D) Inflorescence staminate anthesis. The spathe limb darkening and rotting.

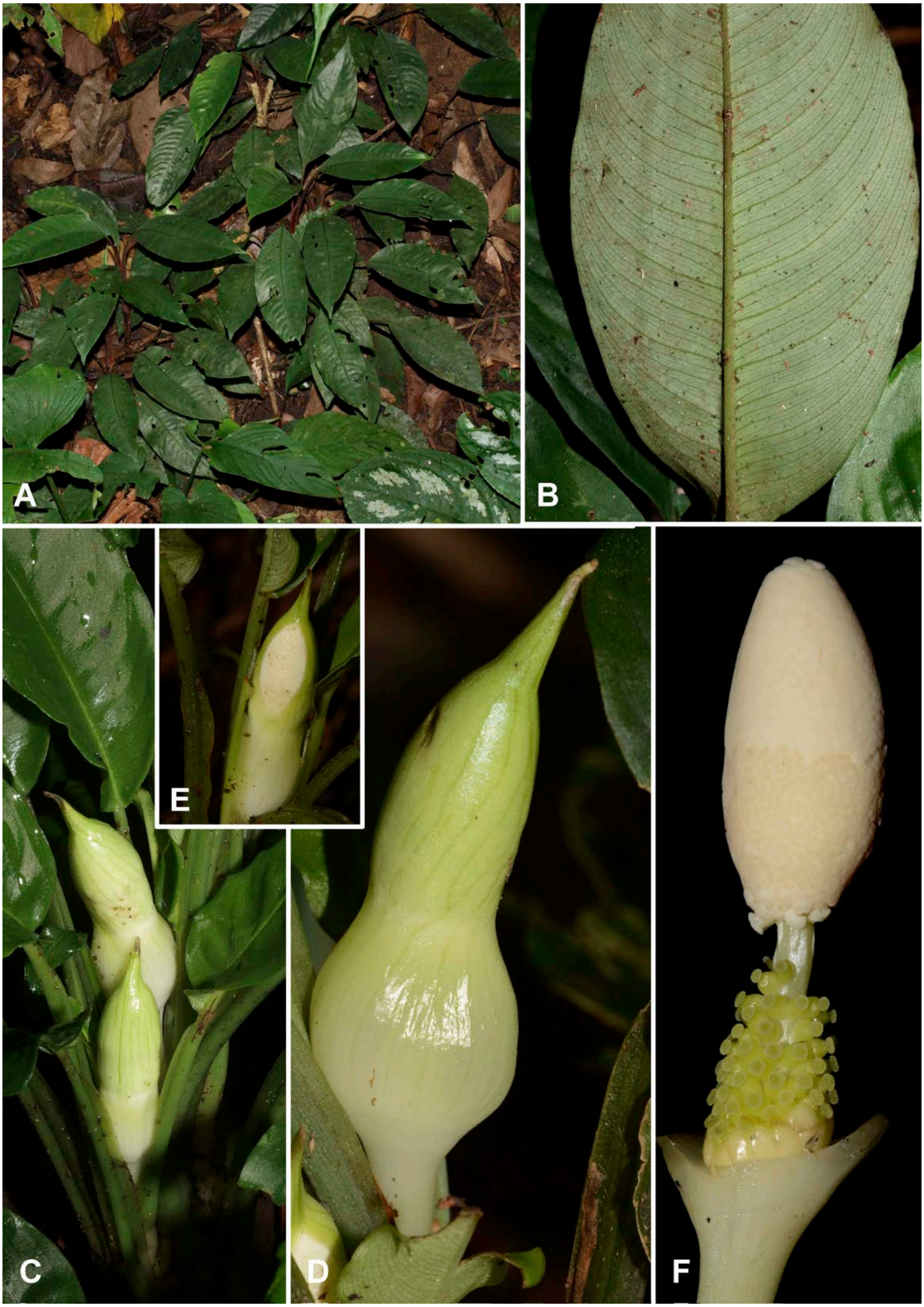

Figure 2. *Schismatoglottis retinervia* (A) Plants in habitat. (B) Leaf blade, abaxial view, showing the typical venation of species of the Schismatoglottis Patentinervia Clade. (C) Flowering shoots. (D & E) Inflorescence at pistillate anthesis; note that the spathe limb hardly opens. (F) Spadix at pistillate anthesis, spathe artificially removed. A & B from *AR–4691*; C – F from *AR-4714*.

Etymology

The trivial epithet is from the Type locality plus the suffix -*ensis*, indicating 'from'.

Distribution

Known only from the type locality on the Sungai Kangkawat, Imbak Canyon Conservation Area.

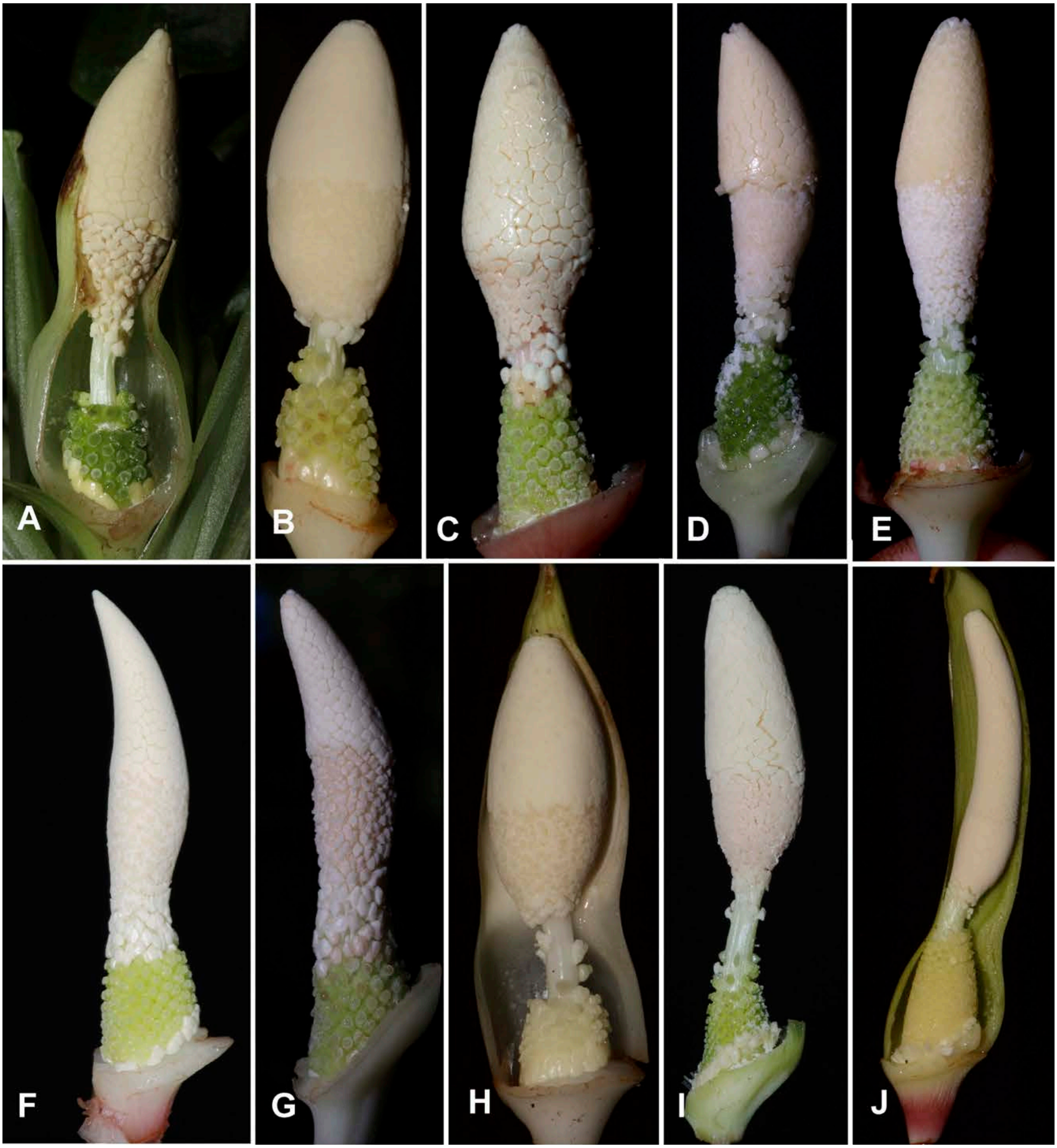

Figure 3. Spadices of 10 species of *Schismatoglottis* Patentinervia Clade compared. (A) *Schismatoglottis imbakensis*. (B) *Schismatoglottis retinervia*. (C) *Schismatoglottis gangsai*. (D) *Schismatoglottis smaragdina*. (E) *Schismatoglottis fossae*. (F) *Schismatoglottis belonis*. (G) *Schismatoglottis gephyra* (H) *Schismatoglottis puncakborneensis*. (I) *Schismatoglottis pichinensis*. (J) *Schismatoglottis gaesa*.

Ecology

Primary lowland mixed dipterocarp forest on Cretaceous Harzburgite and Serpentinite outcrops, occurring on steep muddy river banks above the flood zone, about 270 m asl.

Notes

In Sabah *Schismatoglottis imbakensis* can be mistaken for *S. retinervia*, a species endemic to much higher altitude forest on granite in the Kinabalu area. The two species are readily separated as per the above diagnosis (Fig 1, 2, and 3A, 3B). The stoutly club-like spadix of *Schismatoglottis imbakensis* is most similar to that of *S. gangsai* S. Y. Wong, Aisahtul & P. C. Boyce (Fig. 3C) and *S. smaragdina* S. Y. Wong, Aisahtul & P. C. Boyce (Fig. 3D), both from Pelagus, Kapit, Sarawak, to *S. fossae* S. Y. Wong, Aisahtul & P. C. Boyce (Sarawak: Mulu N.P. - Fig. 3E), *S. puncakborneensis* P. C. Boyce (Sarawak: Kuching, Penrissen Range - Fig. 3H), and to *S. pichinensis* P. C. Boyce (Sarawak: Serian, Padawan karst - Fig. 3I). Recognition of *Schismatoglottis imbakensis* takes the aroid flora of ultramafic substrates in Sabah to six species in four genera – *Alocasia melo* A. Hay, P. C. Boyce & K. M. Wong, *Bucephalandra ultramafica* S. Y. Wong & P. C. Boyce, *Schismatoglottis* (*S. decipiens* A. Hay, *S. imbakensis*, and *S. silamensis* A. Hay), and *Tawaia sabahensis* (S.Y. Wong, S.L. Low & P.C. Boyce) S.Y. Wong & P.C. Boyce. All are restricted to the substrate and furthermore locally endemic.

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Studies on the *Alocasia* Schott (Araceae) of Borneo III: *Alocasia puncakborneensis*, a new species belonging to the Princeps Complex

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Abstract. *Alocasia puncakborneensis* is described and illustrated as a new species of the *Alocasia* Princeps Complex from upper hill forest on the extremely hard Paleogene sandstones of the Penrissen range, SW Sarawak. *Alocasia puncakborneensis* occurs at the highest altitude of any of the locally-restricted /geologically obligated species yet described for the Princeps Complex.

Keywords: *Alocasia* Princeps Complex, Sarawak, Penrissen Range.

INTRODUCTION

Alocasia Schott was last revised for Borneo by Hay (1998), recognizing 20 species of which eight were then described as new, while one probable novelty was left as incompletely known. Since then the incompletely known species was described (Hay 2000), and four entirely new species have been published (Boyce 2007; Kurniawan and Boyce 2011; Wong and Boyce 2016). Presently the *Alocasia* flora for Borneo stands at 24 described species, of which three – *Alocasia longiloba* Miq., *A. princeps* W.Bull, and *A. scabriuscula* N.E.Br. are largely each treated as taxonomically intractable species complexes, with the *A. princeps* and *A. scabriuscula* complexes seemingly related and treated by Hay (1998) together as forming the *A. scariuscula* Group. During the course of fieldwork since 2004 the authors have become aware of at least a further 10 undescribed *Alocasia* species occurring on Borneo but in many instances have yet to encounter the plants in a condition suitable to permit description while herbarium material, where it exists, is wholly inadequate. Occasionally, however, we encounter a new species flowering in habitat permitting formal description.

Here we describe one such novelty occurring on the extremely hard Paleogene sandstones of the Penrissen Range of SW Sarawak where it is

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restricted to moist upper hill forest above 800 m. Geological occurrences in this paper are verified with Tate (2001).

Alocasia puncakborneensis S.Y.Wong & P.C.Boyce, **sp. nov.**

Type: Malaysian Borneo, Sarawak, Kuching, Padawan, Puncak Borneo, trail to Batu Panggah, 1°07'37.0"N 110°13'47.5"E, 838 m asl. 15 May 2019, *Wong Sin Yeng & P. C. Boyce AL- 80* (holotype SAR!; isotype KEP!). (Figures 1 & 2).

Diagnosis

Alocasia puncakborneensis falls uncontroversially in the *Alocasia* Princeps Complex by the thinly leathery leaves, sequentially produced blooms not interspersed with foliage leaves, the staminate portion of the spadix partially enclosed within the lower spathe chamber, and the acroscopic pistils. *Alocasia puncakborneensis* is distinguished from all described species of the complex by the brilliant green leaf blades with the tertiary veins forming a prominently raised fine reticulum on the adaxial surface.

Description

Small herb to ca 55 cm tall; rhizome initially condensed, erect, later elongating and decumbent, ca 3 cm diam.; leaves several together, irregularly interspersed with slightly fleshy pale green, later marcescent brown lanceolate cataphylls to ca 9 cm long; petioles 10–45 cm long, ca 5 mm diam., semi glossy pale green sheathing in the lower ca 10–15%; blades thinly leathery, in adult plants all peltate or mixed peltate and non-peltate, only very occasionally entirely non-peltate, ovate to rather narrowly ovato-sagittate, 10 × 4 cm to 35 × 11–12 cm, widest at or slightly distal to junction of petiole, glossy brilliant green with the adaxial surface densely and finely raised-reticulate; anterior lobe acute, with the tip abruptly acuminate for ca 1 cm; anterior costa with 3–4(–5) primary lateral veins on each side, diverging at ca. 90° proximally, the distal ones at ca 60°, running almost straight to the margin and joining a submarginal vein; axillary glands not conspicuous; secondary venation fine, forming a rather vague interprimary collective vein, very slightly impressed adaxially, flush with the lamina abaxially but slightly darker and thus visible; tertiary veins forming a fine reticulum, prominently raised adaxially, flush abaxially; posterior lobes about 1/5 the length of the anterior, united for 75–90% of their length, or free, when maximally united the base of the blade slightly rounded except for an acute to rather obtuse notch; posterior costae diverging at ca 15° when blade peltate, or at ca 30° when not peltate, so posterior lobes not widely divergent, and naked in the sinus for ca 2 cm; inflorescences 2–4 together, subtended by lanceolate rather fleshy cataphylls, these later briefly marcescent, brown; peduncle ca 10 cm long at anthesis, extending to about twice this during fruiting; spathe ca 6 cm long; lower spathe ca 2 cm long, ovoid, semi glossy white; limb semi glossy white on both surfaces, at first erect, then sharply deflected, oblong lanceolate, mucronate for ca. 6 mm; spadix slightly shorter than the spathe, stipitate for ca 3 mm, stipe semi glossy white; pistillate zone ca 1 cm long; pistillate florets somewhat lax, flask-shaped, ca 1.5 mm diam., facing obliquely upwards, ovary pale green, the stylar region somewhat darker; style slender, ca 0.5 mm long, in a few florets absent; stigma 2-lobed, white and shining/sticky; sterile interstice ca. 4 mm long, slighly attenuated, situated within the chamber of the lower spathe, lower synandrodia irregular in shape, ca. 2 mm diam., upper ones rhombo-hexagonal; staminate zone ca 2 cm long, 4 mm diam., subcylindric, slightly constricted ca 1/3 from the base corresponding to spathe constriction; synandria rhombo-hexagonal ca. 2 mm diam., 4-6-merous, the thecae opening by apical pores, synconnective not expanded beyond the edge of the synandrium; appendix about isodiametric with staminate zone, ca. 2 cm long, gradually tapering to a blunt point, appendical staminodes irregularly polygonal, pale cream; fruiting spathe broadly ovoid, ca. 2 cm long, brilliant white, remaining erect, persistent lower spathe splitting longitidinally into about three segments; berries bright scarlet.

Etymology

The specific epithet is from the Type locality plus the suffix *-ensis*, indicating 'from'. Puncak (summit of a mountain in the Malay language) is pronounced pun-*chak* , with emphasis on the second syllable.

Distribution

Occurring as localised small populations and occasional individuals throughout the higher reaches of the Penrissen Range, never below 800 m, and extending to about 1300 m asl.

Ecology

Terrestrial or facultatively lithophytic on steep shaded slopes or on damp boulders under moist upper hill forest on Paleogene sandstones, between 880–1170 m asl.

Figure 1. *Alocasia puncakborneensis* (A) Plants with fully peltate posterior lobes in habitat. (B & C) Inflorescence at pistillate anthesis. (D) Spadix at pistillate anthesis with the nearside spathe artificially removed. A, unvouchered; B – D from *AL-80*.

Figure 2. *Alocasia puncakborneensis* (A) Leaf blade with posterior lobes none peltate. (B) Leaf blade with peltate posterior lobes. Both unvouchered.

Notes

Alocasia puncakborneensis occurs at the highest altitude of any of the locally-restricted /geologically obligated species yet described for the Princeps Complex. Six of the eight hitherto known species are lowland species, exceptionally occurring up to 600 m asl, and mostly much lower, and are obligated to Karst limestone (Hay 1998). Three of these species occur in Sabah (*Alocasia pangeran* A.Hay, *A. principiculus* A.Hay, *Alocasia puteri* A.Hay), one in east Sarawak (*A. venusta* A.Hay), and two in SW Sarawak (*A. reversa* N.E.Br., *A. ridleyi* A.Hay). One of the remaining species, *Alocasia wongii* A.Hay, occurs across quite a wide area of east Sabah, usually at low altitudes on sandy sedimentary-derived substrates, although occasionally occurring on limestone. As currently defined *Alocasia princeps* W.Bull is widespread throughout middle and east Borneo at up to 1200 m asl, is ecologically highly inconstant, and morphologically rather variable. Detailed field studies will in all likelihood reveal the current concept to consist of more narrowly defined taxa (see Hay 1998 for more detailed discussion).

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Studies on Homalomeneae (Araceae) of Sumatera VI: Two remarkable new species of *Homalomena* [Chamaecladon Clade]

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Abstract. Two ornamental new species of Sumateran *Homalomena* [Chamaecladon] are described: *Homalomena anthurioides* S.Y.Wong, P.C.Boyce & A.Hay and *H. pexa* S.Y.Wong, P.C.Boyce & A.Hay. These novelties represent a continuation of discoveries on Sumatera of species with uniquely, for Asia, highly elaborated epidermis.

Keywords: Araceae, *Homalomena*, Chamaecladon, Indonesia, Sumatera.

INTRODUCTION

The existence on Sumatera of *Homalomena* Schott [Chamaecladon Clade] with extraordinarily ornamented leaf blades and/or petioles has been known since at least the 1920s, Alderwerelt (1922) having described three species with ornamented leaves: *H. asperiifolia* Alderw., *H. cristata* Alderw., and *H. doctersii* Alderw. The past decade has witnessed a marked increase in discovery of such species, among which are some of the most astonishing aroids yet described from the Malay Archipelago.

Previous papers in this series have described six such species (Boyce and Wong 2012; 2013; 2016a,b,c). Here we describe a further two novelties; one with the entire plant densely covered in scale-like hairs, and with the newly emerging leaves and exterior of the spathe with a dense fleece of soft shaggy trichomes, and the other with remarkably stiff and brittle microscopically asperous leaf blades, and petioles with a pronounced proportionately very large apical geniculum.

Both species described here are highly ornamental and have already attracted the attention of horticulturists. For this reason, we are withholding precise information about the type localities.

1. ***Homalomena anthurioides*** S.Y.Wong, P.C.Boyce & A.Hay, **sp. nov.**

Type: Indonesia, Sumatera Utara, South Tapanuli, precise locality withheld for conservation purposes, *Keisuke Hase LA0818-02* (holotype ANDALAS!; isotype SAR!). (Figure 1).

Diagnosis

Homalomena anthurioides is immediately distinguishable from all other described species by the very narrowly elliptic to falcate, stiff and brittle leaf blades held deflexed to almost 90° to the petioles, blades abaxially with alate primary lateral veins, and petioles with a pronounced apical geniculum (ca. 1/5 the length of the petiole). From all other *Homalomena* [Chamaecladon Clade] species *H. anthurioides* is unique these characteristics, and additionally by the spathe pure white at anthesis. From all *Homalomena* with a geniculum terminal on the petiole *H. anthurioides* differs by an unconstricted spathe and pistils with an associated staminode (vs spathe with a constriction concomitant with the top of the pistillate zone and pistils with no associated staminode).

Description

Lithophytic tufted pendulous-leaved herb to ca 15 cm. Stem condensed, in larger plants erect, to ca 5 cm, ca 1 cm diam., shoots pleionanthic; internodes obscured by overlapping leaf bases,. Leaves many together (up to ca 18 per stem); petiole slender, dorsally very narrowly canaliculate, 2–4.5 cm long, ca 1.5 mm diam., about one third the length of blade, sheathing in lower 1/5, with a prominent terminal geniculum ca. 1.5 mm wide, straight or somewhat sigmoid, very minutely asperous, pale grey-green to dull brown-maroon; petiolar sheath fully adnate to petiole, wings triangular, c. 2 cm long, 4 mm wide at base, spread flat, margins somewhat hyaline, greenish to dull brown-maroon; blade deflexed at ca 90° to the petiole, narrowly elliptic-lanceolate, often somewhat falcate, stiffly-leathery and brittle, 6–13 cm long × 2.5–5 cm wide, emerging pale pinkish maroon, maturing to rather pale grey-green, all surfaces very minutely asperous, base broadly cuneate, tip long-acuminate and apiculate for ca 3 mm, midrib slightly impressed adaxially, prominently raised abaxially; primary lateral veins in 3 pairs, diverging at ca 30° from midrib, each pair running into the faint marginal collective vein, slightly impressed adaxially, conspicuously hyaline alate abaxially; interprimaries extremely fine; secondary veins arising from midrib, very fine and not at all alate; tertiary veins forming a faint tessellate reticulum. Blooms up to 3 together opening sequentially in a synflorescence, with a faint resinous odour at anthesis, peduncle semi-erect at anthesis, later declinate; peduncle slender, ca 3 cm long, 1 mm diam., glossy maroon. Spathe ca 1 cm long, ca 5 mm wide across base, oblong, not constricted, pure white, interior glossy white, apex blunt with a terminal mucro to 0.5 mm long, spathe inflating at anthesis and opening by a very narrow longitudinal slit, later closing and enclosing spadix. Spadix ca 9 mm long × 3 mm diam., fertile to tip, sessile; pistillate floret zone ca 2.5 mm long; pistils few, in two or three whorls, cylindric-globose, ca 1 mm tall × 0.7–0.8 mm diam., dirty greenish, stylar region slightly tinged yellowish; stigma sessile, 0.2–0.3 mm diam., producing a large droplet at anthesis; pistillate florets mostly each including one staminode, this ovoid, sessile, ca 0.3 mm diam., waxy white; suprapistillar interstice absent; staminate flower zone ca 6 mm long, stout-conic, apex blunt; stamens densely arranged with groups of 2–3 vaguely arranged into discrete florets, thecae somewhat elongated-globose, ca 0.3 mm long × ca 0.4 mm wide, white, terminal part somewhat translucent, thecae opening by a wide terminal slit; pollen powdery. Fruiting spathe declinate by deflexing of basal portion of peduncle, remaining white. Fruits and seeds not observed.

Etymology

The epithet is formed from *Anthurium*, a genus of Neotropical aroids, and *-oides* – resembling – alluding to the general resemblance of the new species to a miniature pendent-leaved *Anthurium*, in particular the manner in which the petioles have a distinct terminal geniculum, a feature typical of *Anthurium* but very uncommon in *Homalomena*, where in almost all species there is an obscure geniculum about half way to two thirds of the way along the petiole, but very seldom at the tip.

Distribution

Known only from the type locality.

Ecology

Lithophytic on shaded moist banks of fractured metamorphic sandstone above the flood zone of forest streams in humid lowland gallery forest; ca 120 m asl.

Notes

All described *Homalomena* species have a geniculum present on the petiole, in the overwhelming majority of species positioned between half way and two thirds along the petiole, and usually discernible only as a distorted segment of petiole. A very few Bornean species, *Homalomena geniculata* M.Hotta, *H. pseudogeniculata* P.C.Boyce & S.Y.Wong, and *H. punctulata* Engl., are

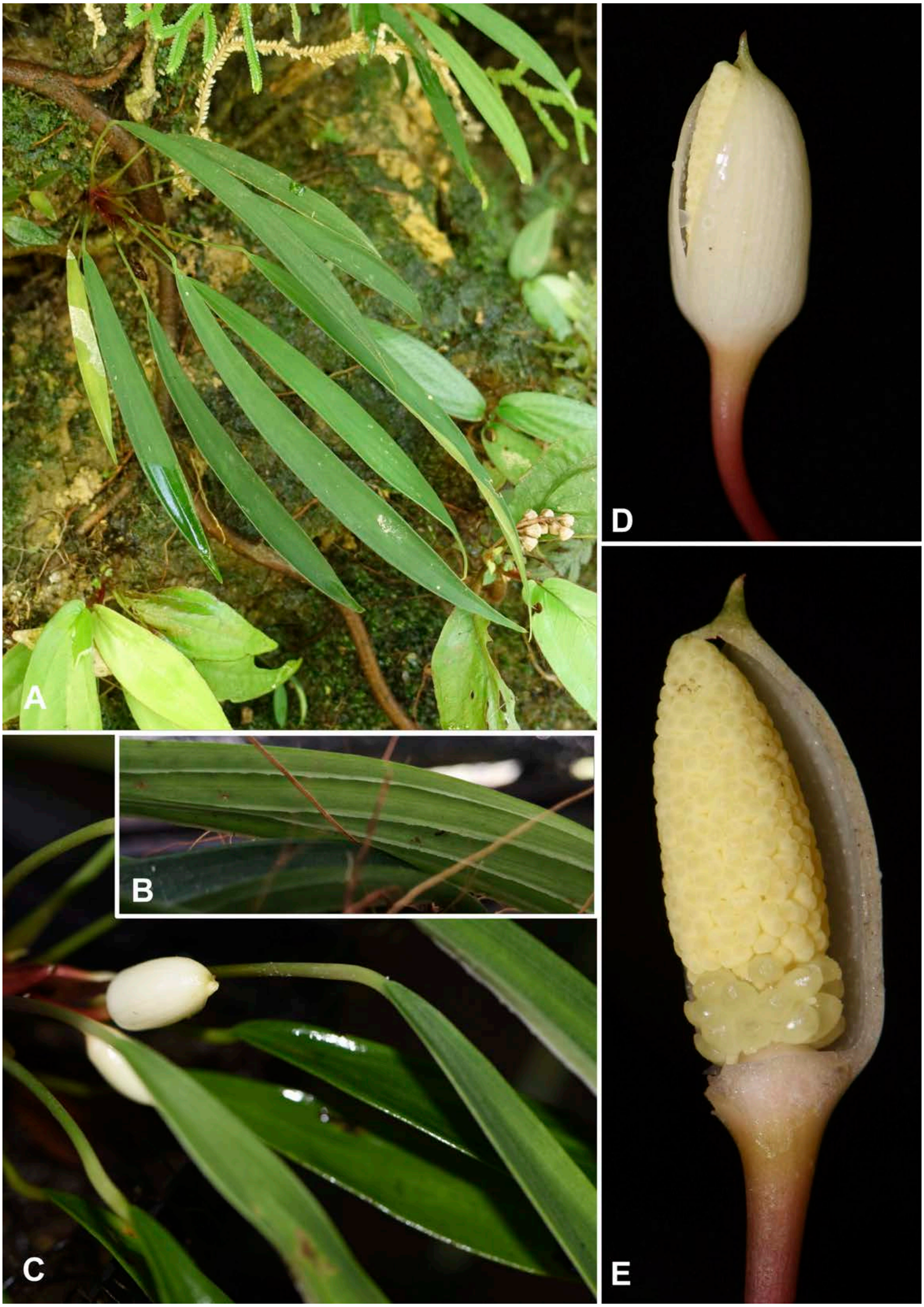

Figure 1. *Homalomena anthurioides* (A) Plant in habitat. (B) Detail of the alate primary lateral veins on the leaf blade abaxial surface. (C) Detail of flowering plant, bloom at late staminate anthesis; (D) Bloom at late pistillate anthesis. (E) Bloom at late pistillate anthesis, nearside spathe artificially removed. All from *LA0818-02*.

remarkable for having the geniculum at the tip of the petiole its junction with the leaf blade, although even in these examples the geniculum is rather obscure.

2. ***Homalomena pexa*** S.Y.Wong, P.C.Boyce & A.Hay, **sp. nov.**

Type: Indonesia, Sumatera Utara, South Tapanuli, precise locality withheld for conservation purposes, *Keisuke Hase LA0818-01* (holotype ANDALAS!; isotype SAR!). (Figure 2).

Diagnosis

Homalomena pexa differs from all other *Homalomena* by combination the entire plant being covered with dense trichomes, with those of the petioles, newly emerging leaves, and spathe exterior forming dense soft shaggy fleece, and the cordate leaf blades. The nearest species in terms of indumentum is *Homalomena hasei* which differs by the much less dense covering of trichomes, the narrowly oblanceolate-elliptic blades abaxially glabrous, and spathe limb glabrous externally.

Description

Lithophytic, occasionally terrestrial rosette-forming herb to ca 7 cm tall and 20 cm across. Stem condensed, ca 3 cm, ca 1.5 cm diam., reddish, shoots pleionanthic; internodes obscured by overlapping leaf bases, not conspicuous. Leaves several together (up to ca 9 per stem); petiole stoutly sub-terete, dorsally somewhat flattened, 7–12 cm long, ca 5 mm diam., ca ½ to about equalling the length of the blade, sheathing in lower 1/5, densely white tomentose with coarse multicellular scale-like hairs; petiolar sheath adnate to petiole, 2–2.5 cm long, wings triangular incurved, dull red; blade oblong- to ovate-cordiform, softy leathery, almost subsucculent, 8–18 cm long × 10–13 cm wide, emerging dull red with very dense tangled scale-like hairs, maturing adaxially rich medium green and densely dirty white tomentose with coarse multicellular scale-like hairs, abaxially green to brownish green, more sparsely hairy, base rounded, posterior lobes blunt, sinus rather narrow, tip acute and apiculate for ca 1 mm, margins rather markedly recurved; midrib impressed adaxially, prominently raised abaxially, tomentose, tinged reddish; primary lateral veins ca 10 on each side diverging at ca 45° from midrib, slightly impressed adaxially, raised, tomentose, and reddish abaxially; interprimaries much finer and more or less alternating with primaries; secondary veins arising from mid-rib and from larger primaries, tomentose; tertiary veins a very faint tessellate reticulum. Blooms up to 9 together in a simple (i.e., one sequence of blooms) synflorescence, without detectable odour, opening sequentially; peduncle semi-erect at anthesis, later declinate, rather stout, ca 4 cm long, 1.6 mm diam., inserted basally (i.e., not obliquely inserted) on spathe, pale red, with dense, pale, recurved tomentum. Spathe ca 3 cm long, ca 1 cm wide across base, not constricted, walls conspicuously thickened, exterior dull red, densely shaggy pale tomentose except for naked portion of spathe overlapped by the outer margin in bud, interior shiny pale pink, apex blunt with a blunt terminal mucro to 1 mm long, spathe inflating at anthesis and opening by a rather wide slit, later closing and enclosing spadix. Spadix ca 2 cm long × 5 mm diam., fertile to tip, stipitate; stipe conical, base flaring, ca 1.5 mm long, 1 mm in diam., creamy pink; pistillate floret zone ca 8 mm long; pistillate florets in three whorls, each comprising a pistil and one staminode, this teardrop shaped with a slender base, ca 0.3 mm diam., waxy creamy white; pistils globose to narrowly flagon-shaped, ca 1 mm tall × 0.7–0.8 mm diam., creamy white; stigma very briefly elevated, 0.2–0.3 mm diam., producing a large droplet at anthesis; staminate florets zone ca 1 cm long, ellipsoid, apex blunt; staminate florets densely arranged, stamens scarcely organized into perceptible florets, thecae ellipsoid, ca 0.4 mm long × ca 0.3 mm wide, cream, terminal part somewhat translucent, thecae opening by a slit extending fully across the theca; pollen powdery. Fruiting spathe declinate. Fruits and seeds not observed.

Etymology

From *pexus* in the feminine, Latin for combed or carded, used relative to the dense indumentum that characterizes the species.

Distribution

Known only from the type locality.

Ecology

Lithophytic or occasionally terrestrial on shaded banks of fractured metamorphic sandstone above the flood zone of forest streams in lowland humid gallery forest; ca 120 m asl.

Notes

The multicellular scaly indumentum of *Homalomena pexa* bears a remarkable resemblance to that of various (very much more robust) neotropical *Philodendron* species, notable among them the well-known *P. squamiferum* Poepp. (Guyanas, N. Brazil), *P. squamicaule* Croat & Grayum (Costa Rica to Ecuador; Figure

Figure 2. *Homalomena pexa* (A) Plant in habitat. (B) Detail of leaf blade abaxial surface. (C) Detail of flowering plant, bloom at late staminate anthesis. (D) Bloom at early pistillate anthesis; note the glabrous band running along the inner margin of the spathe. (E) Synflorescence with one bloom at staminate anthesis (F) Bloom at pistillate anthesis, nearside spathe artificially removed. All from *LA0818-01*.

Figure 3. *Philodendron* cf. *squamicaule,* cultivated in the Jardín Botánico de la Paz y Flora, Bitaco, Colombia, showing a dense multicellular scaly indumentum on abaxial surfaces of the spathes and cataphylls, and on the petioles and peduncles. (Spathe about 30 cm long). Photo A. Hay.

3), and *P. verrucosum* L.Mathieu ex Schott (Costa Rica to Perú), though in these cases not extending onto the leaf blades but nevertheless similarly present on the spathes, peduncles and petioles. Molecular analyses have now well corroborated a close relationship between *Philodendron* and *Homalomena* (e.g. Cusimano et al., 2011; Wong et al., 2013, 2016), in turn suggesting that the presence of such distinctive indumentum in these two genera of the Philodendreae may not be wholly coincidental. Multicellular scaly indumentum is also known in some Bornean species of the less closely allied *Schismatoglottis* (Schismatoglottideae), e.g., *S. ciliata* A.Hay, *S. crinitissima* A.Hay, *S. ferruginea* Engl. and others, but rarely with such multicellular hairs on the blooms (Hay and Yuzammi, 2000).

Homalomena pexa and *H. anthurioides* occur at the same locality, the former favouring damper situations where there is a build-up of soil.

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Two new endemic species of *Monstera* (Araceae: Monsteroideae: Monstereae) from Golfito in southern Costa Rica

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Abstract. *Monstera croatii* M.Cedeño & A.Hay and *M. gambensis* M.Cedeño & M.A.Blanco (Araceae: Monsteroideae: Monstereae) are newly described and illustrated from cantón Golfito in the Pacific lowlands of southern Costa Rica. Notes are provided on how they can be differentiated from similar species. *Monstera croatii* is unique in the genus because it reaches its adult vegetative morphology while growing as a terrestrial plant on the forest floor, and climbs only to a very limited height before flowering. *Monstera gambensis* is one of the smallest species in the genus.

Keywords: Aroids, Central America, Osa Peninsula.

INTRODUCTION

In Costa Rica there are some 24 genera and 256 species of Araceae (including subfamily Lemnoideae, commonly treated as a separate family), the most well-represented of the genera being *Anthurium* Schott, *Philodendron* Schott, and *Monstera* Adans. (Grayum 2003; Ortiz et al. 2018). These groups are abundant and diverse in very humid lowland forests and in cloud forests (Grayum 2003). *Monstera* is a genus that consists mostly of nomadic vines (sometimes referred to as hemi-epiphytes, but see Zotz 2013), and is best known for its often conspicuously perforated leaves (Grayum 2003; Cedeño-Fonseca et al. 2018; Hay 2019). Molecular-phylogenetic analyses of subfamily Monsteroideae agree in finding *Monstera* to be a monophyletic genus most closely allied to the tropical Asian genus *Amydrium* Schott and some (but not all) species of the likewise Asian *Epipremnum* Schott, and it is the only neotropical member of the pantropical tribe Monstereae or '*Rhaphidophora* clade' (Tam et al. 2004; Zuluaga et al. 2019). It is considered one of the taxonomically most poorly understood aroid groups in Mesoamerica (Madison 1977; Croat 1992; Jácome and Croat 2002; Grayum 2003). The most recent taxonomic revision (Madison 1977) recognized 22 species in the entire genus. However, the first author's current research, revising *Monstera* for Central America, indicates that there are more than 40 species in this region alone (Cedeño-Fonseca 2019), with an as yet undetermined number of further species from Mexico, tropical South America, and the Caribbean.

The genus is currently divided into four sections — *Echinospadix* Madison, *Marcgraviopsis* Madison, *Tornelia* (Gutiérrez ex Schott) Madison, and *Monstera* (Madison 1977; Mayo et al. 1997; Croat et al. 2010) — though it is doubtful whether this infrageneric classification will stand up to molecular analysis (*e.g.*, Zuluaga et al. 2019). Section *Monstera* includes, among others, several small, mainly South American species — *Monstera obliqua* Miq. (Costa Rica to Ecuador, Perú, Venezuela, the Guianas and Brazil), *M. xanthospatha* Madison (western Colombia), and *M. minima* Madison (Panama and Colombia) (Madison 1977; Jácome and Croat 2002) — and during recent fieldwork in the forests of La Gamba, Golfito, a new diminutive species was collected, which is described and illustrated here. In addition, a species with terrestrial (or near terrestrial) habit was also collected in Golfito, which only ascends on the phorophyte to about 1.5 m above ground level. This species has also proven to be undescribed, and is named here. It too belongs to sect. *Monstera sensu* Madison (1977).

Monstera croatii M.Cedeño & A.Hay, **sp. nov.**

Type: Costa Rica, Puntarenas Province, Golfito Canton, Golfito, camino hacia las antenas, 8°38'55.1''N, 83°9'30.8''W, 389 m, 4 February 2019 (fr.), *M. Cedeño & A. Hay 1624* (holotype: USJ [2 sheets]). (Figures 1, 2).

Diagnosis

Monstera croatii is recognized by its terrestrial or very low nomadic-vining habit, petioles glaucous at the base, with the sheath extending to about half the total length, the sheath margins involute, and the free portion terete, greyish-glaucous leaf blades, adult leaf blades deeply pinnatifid, peduncles with a persistent mucronate cataphyll, and spadices with more or less spherical basal sterile flowers.

Description

Moderately robust terrestrial herb to appressed nomadic vine, flowering at ca. 0.5–1.5 m above ground level. *Seedlings* not observed. *Juvenile plants* terrestrial; *stem* pale to dark green, smooth, terete, with internodes 1–2.4 cm long by 0.5–1 cm diam.; *petioles* visible (*i.e.*, the blades not shingling), pale to dark green, smooth, 8–10 cm long, sheathed in the lower 3–6 cm, the wings persistent, above the sheath more or less terete to slightly channeled; *leaf blades* not appressed to the substrate, 10–20 × 4–10 cm, lanceolate, narrowed to the base, acuminate at the apex, thinly coriaceous, with or without fenestrations and if fenestrate then generally on only one side and breaking at the margin. *Adult plants* terrestrial and eventually becoming appressed-climbing before flowering; *stem* dark green to pale brown, terete, the internodes 1–1.5 cm long, 1.5–2 cm diam., with pale brown-hairy support and feeder roots; *petioles* rather pale bluish green, glaucous/pruinose, smooth, 34–45 cm long, sheathed in the lower 20–28 cm, with the wings persistent and involute, the free portion terete, slightly canaliculate near the geniculum; *geniculum* more or less terete, very slightly canaliculate adaxially, 2–2.5 cm long; *leaf blades* 30–45 × 25–33 cm, oblong-ovate, rounded to asymmetric at the base, shortly acuminate at the apex, subcoriaceous, deeply pinnatifid but not fenestrate, not decurrent onto the geniculum, glaucous abaxially, the anterior costa canaliculate adaxially, convex abaxially, *primary lateral veins* 8–13 per side, adaxially impressed, abaxially prominent; secondary and tertiary venation parallel; *collective vein* visible at the margins of each lobe; *lobes* 6–12 per side, 0.5–2.5 cm wide, with 1 or 2 primary veins each, sometimes distally bifid. *Inflorescences* on ascending shoots, 1–2 per flowering episode, subtended by basally sheathing, greenish, distally 3-keeled, apically mucronate, persistent cataphylls; *peduncle* smooth, 20–25 cm long; *spathe* acuminate, with two longitudinal keels, membranaceous, light green at pre-anthesis, white-yellowish externally and white internally at anthesis, marcescent after the anthesis, 9–14 × 3–5 cm; *spadix* white in pre-anthesis and anthesis, 6–8 × 2.5–3 cm in early fruit, the basal zone of sterile flowers slender, very conspicuous; *sterile flowers* 3–5 mm long, round with a very prominent stigmatophore; *fertile flowers* 5–6 mm long; *stamens* with laminar filaments 2–5 mm long; *anthers* 1–2 mm de long; *ovary* square-prismatic, 1.5–3 × 1.5–2 mm; *style* squarish, rounded or hexagonal, 0.5–1 × 2–3 mm; *stigma* linear. *Infructescence* with the stylar caps green after anthesis; *mature fruits* not observed; *seeds* not observed.

Etymology

The new species is named for Dr. Thomas B. Croat (MO), the leading authority on neotropical Araceae. He also realized that some herbarium specimens of this spe-

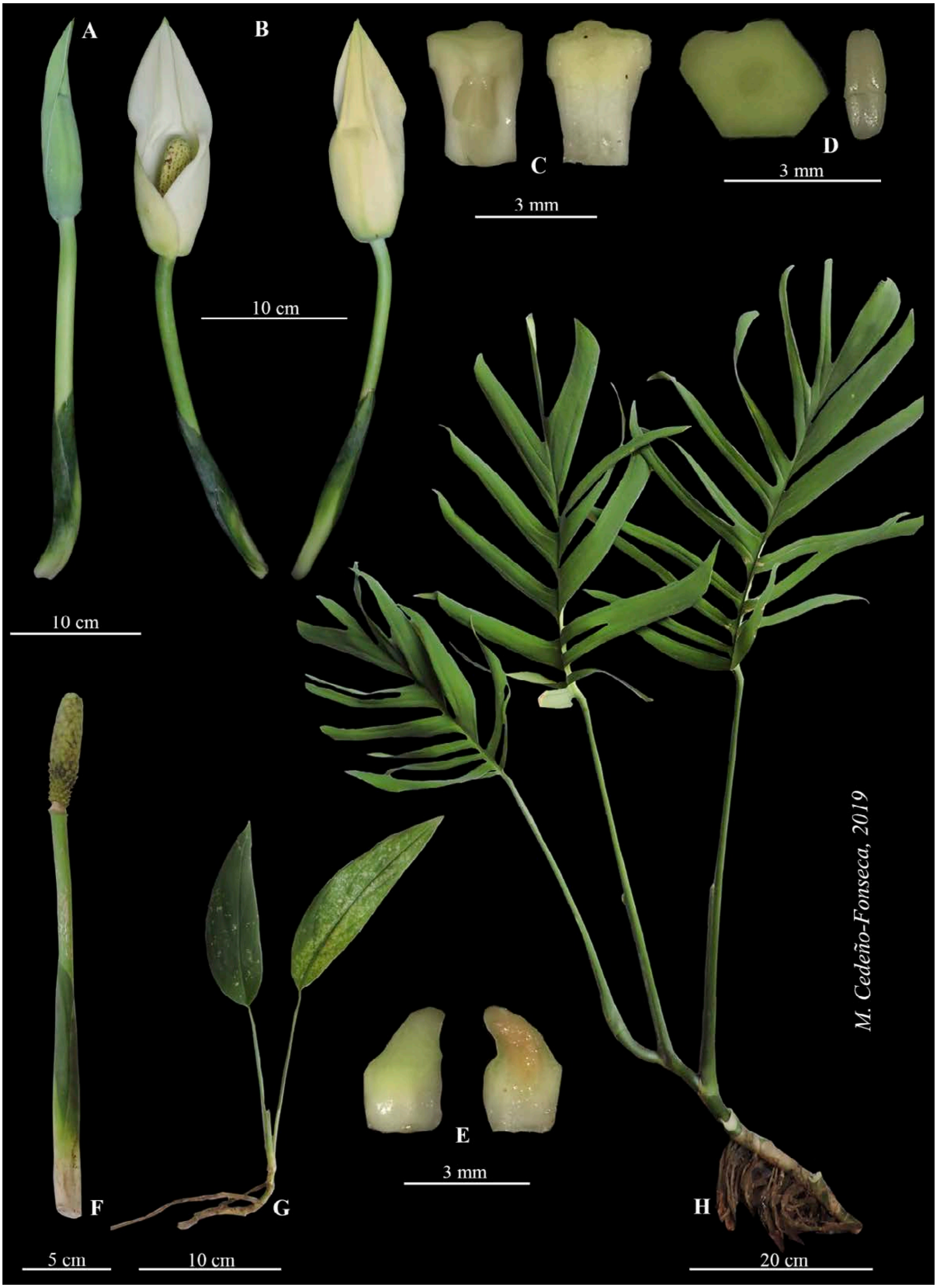

Figure 1. *Monstera croatii*. **A.** Developing inflorescence. **B.** Front and back views of open inflorescence. **C.** Fertile flower in lateral view (left) and in longitudinal section (right). **D.** Stylar plate, top view (left), and individual stamen (right). **E.** Sterile flower in lateral view (left) and in longitudinal section (right). **F.** Infructescence. **G.** Juvenile plant. **H.** Adult plant.

Figure 2. Adult plant of *Monstera croatii* (see description for dimensions). **A.** Hemi-epiphytic habit, ascending to only 1.5 m above the ground, showing the glaucous leaf colour especially on the youngest leaves. **B.** Terrestrial habit, with the same morphology as that of reproductive individuals. **C.** Young infructescences with the green stylar layer, conspicuous basal sterile zone, and persistent subtending cataphylls. **D.** The base of the glaucous/pruinose petiole and persistent involute petiole sheath (arrow). **E.** Part of the petiole completely terete beyond the sheath. **F.** Leaf with two primary veins per lobe, sometimes bifid into lobules that divide up to 4 cm away from the costa (arrow). Photographs: M. Cedeño-Fonseca.

cies, previously identified as *M. pinnatipartita* Schott, could represent a different, undescribed species.

Distribution and habitat

Monstera croatii is endemic to Costa Rica, where it is known only from the south on the Pacific side in the region of Golfito and the Parque Nacional Corcovado (both in the cantón of Golfito) at ca. 300–600 m, in primary and secondary forest and in open areas (Figure 6).

Phenology

Immature infructescences recorded in February; flowering observed in October and November.

Conservation status

Monstera croatii is protected in the Refugio Nacional de Vida Silvestre Golfito and in the Parque Nacional Corcovado.

Notes

Monstera croatii is differentiated from all other Costa Rican species of *Monstera* by having pruinose/glaucous stems and petioles, the petioles sheathing for about half their length, with the sheath wings involute and persistent and the free (distal) part terete or only weakly channeled. It is further differentiated by the deeply pinnatifid and bluish green leaf blades, sometimes with bifid lobes, and the pruinose peduncles with a persistent sheathing mucronate cataphyll.

A unique characteristic of this species is its terrestrial habit, reaching the adult vegetative stage in this state and climbing only to very limited height before flowering. Fertile terrestrial individuals were not found, but one plant was observed fertile after climbing only 50 cm above ground level with the same stem and leaf morphology as terrestrial examples.

Monstera croatii has sterile flowers with the ovary spherical, as is also the case in *M. glaucescens* Croat & Grayum, which too has glaucous stems and briefly sheathed petioles, but that species (known only from the Caribbean side of Costa Rica) has the leaves pinnately lobed (never deeply pinnatifid), the petiolar sheath persistent but not with involute margins, and the non-sheathing part of the petiole channeled (never terete). *Monstera croatii* can also be confused with *Monstera pinnatipartita,* but that species has the petioles green or speckled (never glaucous), never develops to the adult vegetative form on the ground, is fertile only after significantly ascending its phorophyte, and has acuminate and marcescent (not mucronate and persistent) cataphylls.

Additional specimens studied (Paratypes):

COSTA RICA. Puntarenas, Golfito, Golfito, camino hacia las antenas, 8°38'55.1"N, 83°9'30.8"W, 389 m, 4 February 2019 (fr.), *M. Cedeño & A. Hay 1625* (USJ [2 sheets]). Puntarenas, Golfito, Golfito, camino a las torres del I.C.E., aprox. 2 km antes de llegar, 8°39'25"N, 83°9'25"W, 389 m, 29 January 1992 (fr.), *Á. Fernández 205* (CR, MO [3 sheets]). Puntarenas, Golfito, Parque Nacional Corcovado, Estación Agujas, Cerro Rincón, 8°31'34.467"N, 83°28'3.9"W, 600 m, 11 November 1999 (fl.), *E. Mora 725* (CR [2 sheets]).

Monstera gambensis M.Cedeño & M.A.Blanco, **sp. nov.**

Type: Costa Rica, Puntarenas Province, Golfito Canton, Golfito, La Gamba, sendero sobre quebrada, 8°41'02" N, 83°12'15"W, 94 m, 27 May 2016, *M. Cedeño, A. P. Karremans & I. Chinchilla 890* (holotype: USJ) (Figures 3, 4, 5).

Diagnosis

Monstera gambensis is recognised by its small entire leaves with or without fenestrations, and its asperous petioles with involute sheath margins that appear whitish. Similar in size to *Monstera obliqua*, it differs from that species by having asperous (vs. smooth) petioles, with the sheath margins persistent (vs. completely deciduous), and smaller leaf blades (12–24 × 5–10 cm, vs. ca. 35 × 14 cm).

Description

Nomadic vines, fertile at ca. 2 m above the ground. *Seedlings* unknown. *Juvenile plants* appressed-climbing; *stem* dark green, slightly rough, internodes 3–5 cm long, 4–10 mm diam.; *petioles* visible (*i.e.*, the leaves not shingling), dark green or light, slightly rough, 3–5 cm long, sheathed to the base of the geniculum, the wings persistent; *leaf blades* more or less horizontal, not flattened to the substrate of the phorophyte, 4–7 × 3–4 cm, obovate or lanceolate, subcordate to truncate at the base, acuminate at the apex, thinly coriaceous, without fenestrations. *Adult plants* appressed-climbing; *stem* terete, dark green, rough, internodes 1–4 cm long, 5–10 mm diam.; supporting *roots* black and corky, 4–6 cm long, feeder roots black and semi-corky, both with black root hairs; *leaves* numerous, sub-erect; *petioles* light green or whitish, rough to the geniculum, 17–22 cm long, sheathed to 2–3 cm below the base of the geniculum with the wings involute and persistent, the free portion slightly grooved; *geniculum* elongated, 0.5–1 cm long; *leaf blades* 12–24 × 5–10 cm, lanceolate, attenuate and decurrent on the

Figure 3. *Monstera gambensis*. **A.** Adult plant showing leaves without perforations. **B.** Cross-section of petiole showing involute sheath wings. **C.** Juvenile plant. **D.** Petiole of adult plant with persistent sheath and involute sheath wings. **E.** Mature infructescence with persistent cataphylls at the base. Illustration by Sara Díaz Poltronieri.

geniculum at the base (the decurrent part 0.5–1 mm wide), acuminate at the apex, without or (less commonly) with fenestrations (when present, one to two perforations close to each other on the same side of the blade near its middle part), often only one side fenestrated, with entire margins, subcoriaceous; anterior costa chan-

Figure 4. *Monstera gambensis*. **A.** Adult plant with non-perforated leaves. **B.** Juvenile plant. **C.** Adult leaf with two perforations. Photographs: M. Cedeño-Fonseca.

neled adaxially, convex to the middle of the blade abaxially, slightly rough, with 5–13 primary lateral veins on each side, impressed or indistinct abaxially, prominent on the underside, collective vein not visible. *Inflorescences* on ascending stems; *peduncle* rough throughout, 20–25 cm long; *spathe* unknown; *spadix* 7–10 × 1.3–1.6 cm, colour at and before anthesis unknown; *sterile flowers* 3–4 mm long; *fertile flowers* 4–5 mm long; *stamens* with laminar filaments 2–4 mm long; *anther* 1–2 mm long; *ovary* prismatic, longitudinally ribbed, 2–3 × 2–3 mm; *stylar region* hexagonal, 1–2 × 3–5 mm; *stigma* linear. *Infructescence* yellow when ripe; *fruits* with white pulp; seeds black, 2–3 mm long.

Etymology

The epithet *gambensis* refers to the type locality.

Distribution and habitat

Monstera gambensis is endemic to Costa Rica, where it has been found growing low on the supporting trees (ca. 2 m above ground level), in rain forest at La Gamba Biological Station, cantón Golfito, mostly at 50–100 m. (Figure 6).

Phenology

Flowering has not been observed. An infructescence was recorded in May.

Conservation status

It is protected at the La Gamba Biological Station, the only known locality for this species.

Notes

Monstera obliqua, a species whose type is from Surinam and which in its current, broad conception extends into Amazonia, is known in Costa Rica only from the southeastern corner of the country (Grayum 2003), while the Costa Rican endemic *M. gambensis* is known only by a single collection from La Gamba, Golfito. *Monstera gambensis* is one of the smallest species in the genus,

Figure 5. *Monstera gambensis*. **A.** Support roots (***i***) and a feeding root (***ii***) both corky and blackened. **B.** Petiole sheath margins persistent and involute in adult plants (arrow). **C.** Petioles with sheath margins persisting, whitish and asperous (arrow). **D.** Internodes of adult plant (arrow). **E.** The shallowly channeled distal portion of the petiole (arrow). **F.** Portions of either dead epidermis or epicuticular waxes that give a whitish appearance and an asperous texture to the surface of the petioles. Photographs: M. Cedeño-Fonseca.

together with *M. obliqua* and *M. minima*. The latter, with smaller petioles (2–6 cm), leaf blades (9–14 × 2–4 cm), and spadices (ca. 4.4 × 09–1 cm) even smaller than those of *M. gambensis* (Jácome & Croat 2002), is only known from the northern (Caribbean) coast of Panama and along the Pacific slope of northern Colombia, in the

Figure 6. Distribution of *Monstera croatii* (triangles), in Golfito and Corcovado National Park, and *M. gambensis* (circle), in Golfito, Costa Rica.

Chocó region (Jácome and Croat 2002). In Costa Rica, *M. gambensis* is found in lowland tropical wet forest at elevations of up to ca. 100 m. The individuals observed were climbing in the undisturbed forest on small trees no more than 2.5 m high, with abundant shade in the understorey.

Most adult leaves of *Monstera gambensis* are not fenestrated, but occasionally leaves are produced with up to two perforations, close to each other on the same side of the blade near its middle part. The measurements for the flowers of *M. gambensis* given above were taken from flower remnants of a single fruiting spadix, so they should be interpreted with caution.

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Review

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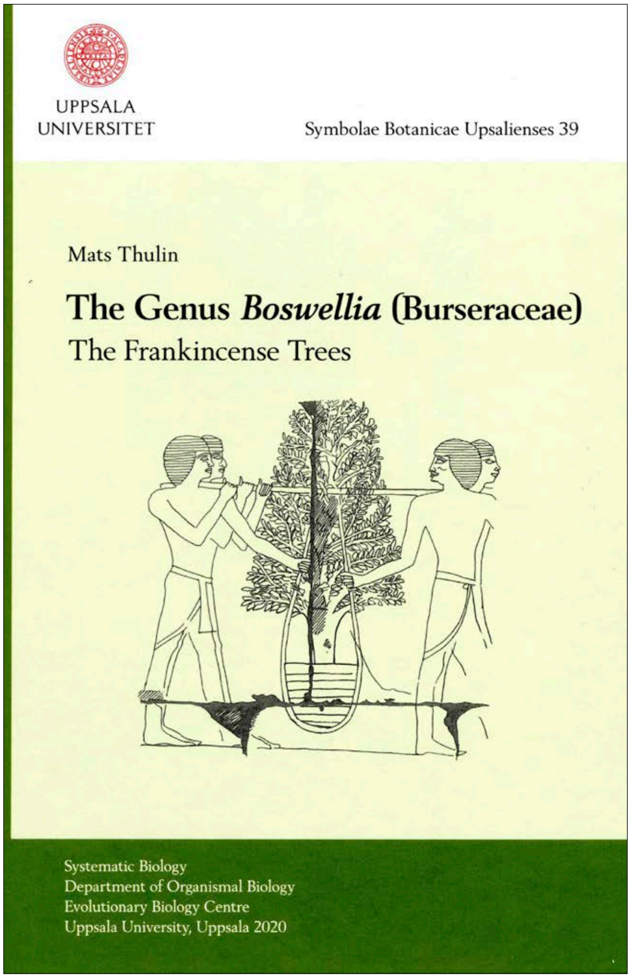

UPPSALA UNIVERSITET

Symbolae Botanicae Upsalienses 39

Mats Thulin

The Genus *Boswellia* (Burseraceae)

The Frankincense Trees

Systematic Biology
Department of Organismal Biology
Evolutionary Biology Centre
Uppsala University, Uppsala 2020

Among the contributions on the Flora of Horn of Africa this book on the Frankincense Trees here reviewed represents an excellent example of taxonomic research carried out over a period of decades by Prof. Thulin, recently retired from the University of Uppsala, but still active.

Let me come back to few decades ago in 1999, when I visited the Soqotra Archipelago (Yemen), a 40-day expedition together with the former curator of the Tropical Herbarium (FT) of Florence, Marcello Tardelli. In addition to the beauty of the landscape and the friendliness of inhabitants, what fascinated me was the incredible biological diversity of the Archipelago, and its high rate of endemism. Among the most interesting genera, such as *Croton*, *Dendrosycios*, *Dracaena*, *Euphorbia*, *Hypericum*, and many others, *Boswellia* had a special impact not only due to its naturalistic and taxonomic value, but also for its cultural meaning, considering the historical-religious and symbolic role of frankincense tree in ancient cultures from the Egyptians to the present day. As soon as I knew about this contribution on the genus *Boswellia*, it awakened an extreme interest in me, considering the experience and competence of the writer.

The author reminds to have met the Frankincense Trees for the first time in September 1975 during a collecting trip to Ethiopia, and subsequently to Kenya. The turning point was on the occasion of the Somali-Swedish project on the production of incense in Somalia that permitted the study of natural populations in crucial areas such as Somaliland, and southern Arabia. Of crucial importance were the nineties, during which Mats Thulin carried out a careful study of *Boswellia* in the Soqotra Archipelago and southern Arabia, thus covering the entire distribution area in the African-Arabic area. So we can deduce that this work is part of 45 years of taxonomic research in the Horn of Africa and Arabic peninsula, a period that also saw the publication in four volumes of the *Flora of Somalia*, written and edited by the same author.

The book begins with a historical retrospective on the meaning of incense from the Egyptians to recent times, through the Greeks, Romans, and the Middle Ages, having represented a commercial product of high practical and symbolic value, especially in the Chris-

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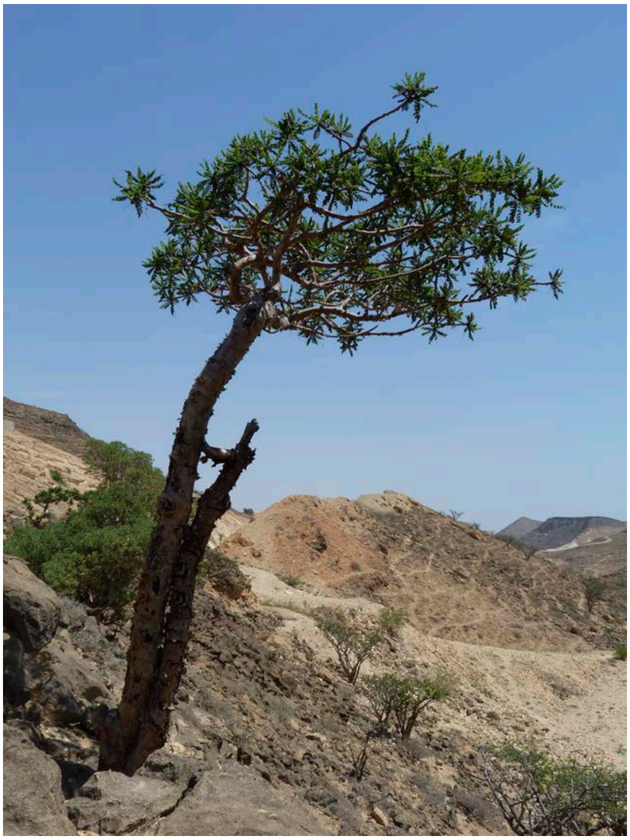

Boswellia sacra Flück**.** (Sultanate of Oman, Dhofar, wadi area near Mughsayl (photo: 2015, Lia Pignotti).

tian, Islamic liturgies and in the Ethiopian Orthodox Church. The Royal Danish Expedition to Egypt and Yemen (*Arabia Felix*) between 1761 and 1763 is also remembered. This expedition had the aim of investigating the origin of the various products mentioned in the Bible, including incense. A taxonomic description of the genus *Boswellia* follows, focusing on the major contributors of the past, such as Balfour, Guillaumin, Hutchinson, Chiovenda, Engler, Capuron, Hepper.

Particular importance is placed on the phylogeny of the genus *Boswellia*, recently studied and supported as monophyletic with the exception of the genus *Ambilobea* of Madagascar, focusing on three areas of differentiation: an Indian clade, an African clade, and a Soqotran clade, the latter represented by the largest number of species (seven). In the phylogenetic and phylogeographical scenario of the genus *Boswellia*, the archipelago of Soqotra is definitely the most interesting area of its evolutionary radiation.

The introduction to the genus *Boswellia* begins with a detailed description, followed by information on the following aspects: geographical distribution, morpho-anatomical characters, growth, reproductive biology and pollination, dispersion, cytology, hybridization, conservation, uses, and incense harvesting and processing.

The chapters dedicated to each species are preceded by a general identification key.

Type information of accepted names and synonyms is included, in many cases with comments on nomenclature. New lectotypes are also designated. Distribution, vernacular names and uses, IUCN Red List assessment, and taxonomic remarks are reported.

Herbarium specimens are grouped by geographical area and transcribed in detail. In many cases, line drawings are provided. The original photo documentation of the author and his close collaborators is also fundamental for understanding the environment where the species described in the text live.

A total of 24 *Boswellia* species are presented, including 2 new species: ***Boswellia samhaensis*** Thulin & Scholte (Samha island, Soqotran Archipelago), ***Boswellia scopulorum*** Thulin (Soqotra). A "new" species still under study, *Boswellia* "*hesperia*" **sp. prov**. from Soqotra is proposed as related to *Boswellia popoviana* Hepper, also from Soqotra Island. Last but not least a new combination is proposed: ***Boswellia aspleniifolia*** (Balf. F.) Thulin., **comb. nov**.

"*Species excludendae*" amounts to 7, all referable to genera different from *Boswellia* such as *Canarium*, *Dysoxylum*, *Garuga*. Particular critical attention is paid to *Boswellia bricchettii* (Chiov.) Chiov. An updated and useful bibliography for future investigations on *Boswellia* is listed at the end of the book.

This work by Mats Thulin represents a turning point in the knowledge of one of the most interesting paleotropical genera extending from Mali and Burkina Faso to west India, through the Ethiopian / Arabic area.

What makes us proud of this contribution is the recognition it gives to the University of Florence with the Tropical Herbarium FT, which has received the author for many years as a frequent and precious visitor.

This, this book — distinguished by the rigor with which it was conceived and then realized after years of study — is an example of how a monograph should be written: a clear message in a current editorial scenario in which, many times, improvisation and science publication frenzy led to poor results in Plant Taxonomy.

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