

# *Englerarum* (Araceae, Aroideae): a new genus supported by plastid and nuclear phylogenies

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**Abstract** The new monotypic genus *Englerarum* Nauheimer & P.C.Boyce, with the only species *Englerarum hypnosum* (J.T.Yin, Y.H.Wang & Z.F.Xu) Nauheimer & P.C.Boyce, is here described. The new combination of *Alocasia hypnosa* J.T.Yin, Y.H.Wang & Z.F.Xu, with exclusion of *Alocasia* (Schott) G.Don and transfer into *Englerarum*, is based on molecular phylogenies using plastid and nuclear data. The plant occurs on forested limestone outcrops in tropical and subtropical continental Southeast Asia, ranging from Southwest China, through the Lao PDR, and into North and Southeast Thailand. *Englerarum* represents an isolated lineage in the basal *Pistia*-clade. Its inclusion into the phylogenetic framework provides new insights into the evolution of this clade, and into the morphological characters used to distinguish the close related genera *Alocasia* and *Colocasia*.

**Keywords** *Alocasia hypnosa* · Colocasioideae · Limestone · Southeast Asia · SW China

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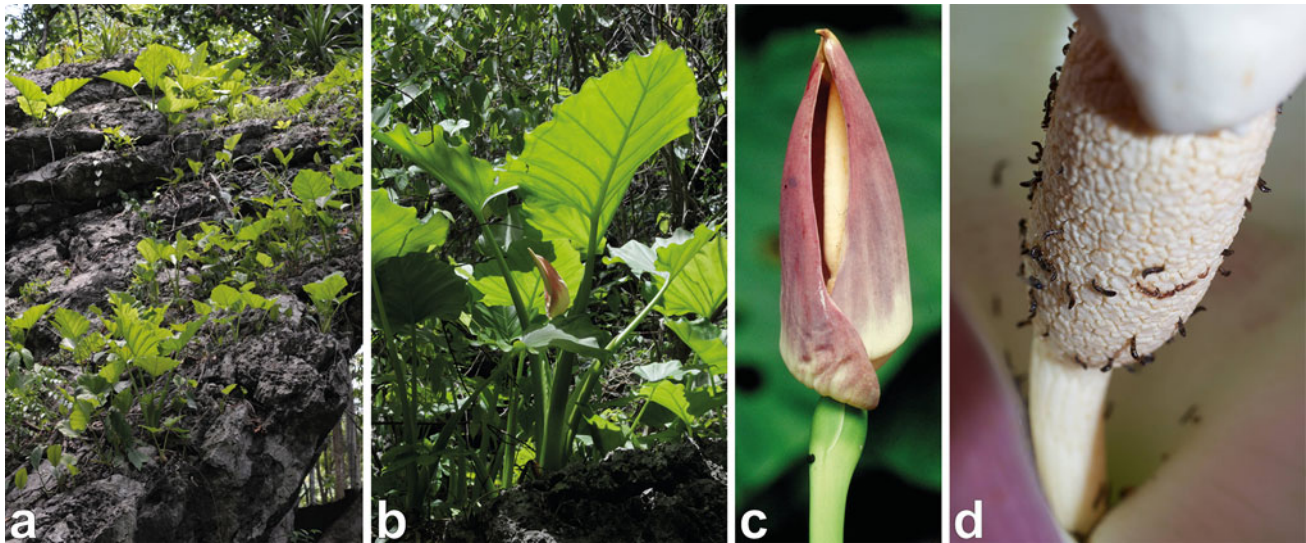
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## Introduction

The number of recognized genera in the family Araceae has increased in the last few years from 105 (Mayo et al. 1997) to 118. Reasons for this, besides for the inclusion of the duckweeds (as Lemnoideae) in the family, are the discovery of new species of e.g., *Pichinia* P.C.Boyce & S.Y.Wong (Wong and Boyce 2010b) and *Lorenzia* E.G.Gonç (Gonçalves 2012) and new taxonomic work on the highly speciose Schismatoglottideae group (Boyce and Wong 2008; Wong and Boyce 2010a, c). In addition, new molecular phylogenetic studies have shown the non-monophyly of already described genera and resulted into new combinations such as in *Croatiella* E.G.Gonç, *Incarum* E.G.Gonç (Gonçalves 2005), and *Typhonium* Schott (Cusimano et al. 2010). Molecular analyses of four plastid regions (*trnL*, *trnL-F*, *trnK/matK*, and *rpl20-rps12*) and one nuclear gene (*phyC*) revealed that the species described as *Alocasia hypnosa* J.T.Yin, Y.H.Wang & Z.F.Xu has to be excluded of *Alocasia* (Schott) G.Don to maintain the monophyly of *Alocasia* (Nauheimer et al. 2012a). Plastid and nuclear phylogenies both corroborated that *A. hypnosa* is not a part of any closely related genera, but represents its own and separate lineage next to the four major clades in the *Pistia*-clade (sensu Cusimano et al. 2011), the *Colocasia*-clade (comprising *Ariopsis* J.Graham, *Colocasia* Schott, *Remusatia* Schott, and *Steudnera* K.Koch), the *Areae*-clade (comprising the tribes *Areae* and *Arisaemateae*), and the *Alocasia*-clade (*Alocasia* and *Leucocasia* Schott).

*Alocasia hypnosa* is a lithophytic or occasionally terrestrial herb up to 1 m in height (Fig. 1). It occurs on humid ledges, exposed areas of forest regrowth, and deciduous, bamboo-dominated forest on karst limestone at an altitude of approximately 800–1,000 m (Fig. 1a). *Alocasia hypnosa* ranges from SW China (type locality) to the Lao PDR, and



**Fig. 1** *Englerarum hypnosum* (J.T.Yin, Y.H.Wang & Z.F.Xu) Nauheimer & P.C.Boyce. **a** Habitat, several plants growing on limestone in Thailand; **b** single plant with inflorescence; **c** close-up of

inflorescence. **d** spadix visited by numerous staphylinid beetles. Photo courtesy of David Prehler (photos a and b) and John Mood (photo d)

N and SE Thailand. It has prominent stolons for vegetative reproduction that enable colonization on almost vertical limestone cliffs. Wang et al. (2005) described this species based on a collection from southern Yunnan, China. The species was assigned to *Alocasia* based on overall similarity to *Alocasia odora* K.Koch. Two morphological characters distinguish *A. hypnosa* from all other *Alocasia* species; the absence of wax glands in the axils of the primary veins on the abaxial surface of the leaf blade, and the production of long stolons with tubercles for vegetative reproduction. Further *A. hypnosa* has a fully deciduous habit, which is unusual for *Alocasia*, and a protracted leafless resting phase, which is unknown in *Alocasia*. *Alocasia hypnosa* was also compared to species of the morphologically similar *Colocasia*; however, the two genera differed in the type of placentation and their fruits (Hay 1998).

Here, we use nuclear and plastid data to show that *A. hypnosa* does not group with *Alocasia* or with any other closely related genus, but instead represents an isolated lineage in the *Pistia*-clade. We propose a new genus for the family Araceae in the subfamily Aroideae: *Englerarum* Nauheimer & P.C.Boyce, a new combination for this species, *Englerarum hypnosum* (J.T.Yin, Y.H.Wang & Z.F.Xu) Nauheimer & P.C.Boyce.

## Materials and methods

### Sampling

*Pistia stratiotes* L. and *Protarum sechellarum* Engl. were used as outgroup taxa based on Nauheimer et al. (2012b)

along with 28 species representing all genera of the *Pistia*-clade of the Aroideae. Multiple accessions of *Alocasia* and *Colocasia* were included. Sequences of four chloroplast loci, the *trnL* intron, the *trnL-F* intergenic spacer, the *rpl20-rps12* intergenic spacer, the *trnK/matK* region, as well as of one nuclear gene, *phyC* (Nauheimer et al. 2012a) were analysed. Voucher information and GenBank numbers for all accessions are shown in Table 1.

### Alignment and phylogenetic analyses

The sequences were aligned manually using the package Geneious (5.0). To infer phylogenetic relationships, we applied maximum likelihood (ML) optimization with the software RAXML (7.3.2, Stamatakis 2006) and RAXML-Gui (Silvestro and Michalak 2012), as well as a Bayesian approach with the software MrBayes (3.2.1; Ronquist and Huelsenbeck (2003)). The analyses were performed using the generalized time-reversible substitution model with gamma rate heterogeneity. To capture the potential information of indels and gaps that exist in the chloroplast data, a multistate matrix was compiled with the software Seq-Stat (1.4.1; Müller 2005) using modified complex indel coding. This matrix was analysed as separate partition together with the DNA matrix using maximum likelihood optimization and the multigamma model in RAXML. Statistical support was assessed via 1,000 bootstrap (BS) replicates for the ML approaches and via posterior probabilities (PP) for the Bayesian approach. Throughout this paper, BS values of 70–84 % and PP of 0.9–0.95 support are considered as moderate, a BS value of 85–100 % and PP of 0.95–1 is considered as strong support.

**Table 1** List of accessions including species names, voucher information, and GenBank numbers for all used loci

Name	Voucher	<i>trnL</i>	<i>trnL-F</i>	<i>trnK/matK</i>	<i>rpl20-rps12</i>	<i>phyC</i>
<i>Alocasia cucullata</i> (Lour.) G. Don	J. Bogner 2638 (M)	JQ238656	JQ238738	JQ238824	JQ238910	JQ083506
<i>Alocasia macrorrhizos</i> (L.) Don	M. Medecilo 435 (De La Salle University Dasmariñas Herbarium)	JQ238671	JQ238756	JQ238841	JQ238925	JQ083523
<i>Alocasia melo</i> A. Hay, P. Boyce & K. Wong	C. Lee AL-61 (SAR)	JQ238673	JQ238758	JQ238843	JQ238927	JQ083525
<i>Alocasia nycteris</i> Medecilo, G. C. Yao & Madulid	M. Medecilo 458 (De La Salle University Dasmariñas Herbarium)	JQ238678	JQ238763	JQ238847	JQ238930	JQ083529
<i>Alocasia ridleyi</i> A. Hay	J. Bogner 2735 (M)	JQ238690	JQ238776	JQ238860	JQ238942	JQ083542
<i>Ariopsis protanthera</i> N.E. Br.	H. Hara, S. Kurosawa, H. Ohashi 69578 (TI)	AY248985	AY248947	EU886587	AY248910	JQ083567
<i>Arisaema speciosum</i> (Wall.) Mart.	W. Hettterscheid H.AR. 294					
<i>Arum italicum</i> Mill.	BG Mainz 20Jul2001	AY248997	AY248959	EU886517	AY248922	EU886472
<i>Biarum davisii</i> Turrill	T. Croat 78231 (MO)	AY248998	AY248960	EU886525	AY248923	EU886479
<i>Colocasia esculenta</i> (L.) Schott	J. Bogner 2958 (M)	JQ238718	JQ238804	JQ238890	JQ238972	JQ083569
<i>Colocasia fontanesii</i> Schott	J. Bogner 2215 (M)	JQ238720	JQ238806	JQ238892	JQ238974	JQ083570
<i>Colocasia menglaensis</i> J. T. Yin, H. Li & Z. F. Xu	J. Bogner 2274 (M)	JQ238722	JQ238808	JQ238894	JQ238976	JQ083572
<i>Dacunculus vulgaris</i> Schott	T. Croat 78286 (MO)	AY249002	AY248964	EU886532	AY248927	EU886476
<i>Eminium spiculatum</i> (Blume) Schott	BG Bonn 15031	AY249003	AY248965	EU886530	AY248928	EU886474
<i>Englerarum hypnosum</i> J.T.Yin, Y.H.Wang & Z.F.Xu	D. Prehler 175 (WU)	JQ238662	JQ238746	JQ238831	JQ238916	JQ083582
<i>Helicodiceros muscivorus</i> (L. f.) Engl.	T. Croat 71821 (MO)	AY249004	AY248966	EU886533	AY248929	EU886480
<i>Lazarum brownii</i> Schott	W. Hettterscheid HAR43	AY249013	AY248975	EU886538	EU886607	EU886492
<i>Leucocasia gigantea</i> (Blume) Hook.f.	J. Bogner 427 (M)	JQ238721	JQ238807	JQ238893	JQ238975	JQ083571
<i>Pinellia ternata</i> (Thunb.) Ten. ex Breitenb.	J. McClemens s.n. 30 Jul 2001	AY249006	AY248968	EU886503	AY248931	JQ083574
<i>Pistia stratiotes</i> L.	J. Bogner 2705 (M)	AY249007	AY248969	EU886585	AY248932	JQ083575
<i>Protarum sechellarum</i> Engl.	J. Bogner 2545 (M)	JQ238724	JQ238810	–	–	JQ083576
<i>Remusatia vivipara</i> (Roxb.) Schott	J. Bogner 2982 (M)	JQ238726	JQ238812	JQ238897	JQ238979	JQ083578
<i>Stuednera assamica</i> Hook. f.	J. Bogner 2588 (M)	EF517219	EF517214	JQ238898	EF517224	JQ083579
<i>Stuednera kerrii</i> Gagnep.	J. Bogner 1891 (M)	EF517218	EF517213	JQ238899	EF517223	JQ083581
<i>Therophonum dalzellii</i> Schott	P. Bruggemann 168	AY249011	AY248973	EU886534	AY248936	EU886486
<i>Typhonium trilobatum</i> (L.) Schott	J. Murata 5	AY249016	AY248978	EU886571	AY248941	EU886496

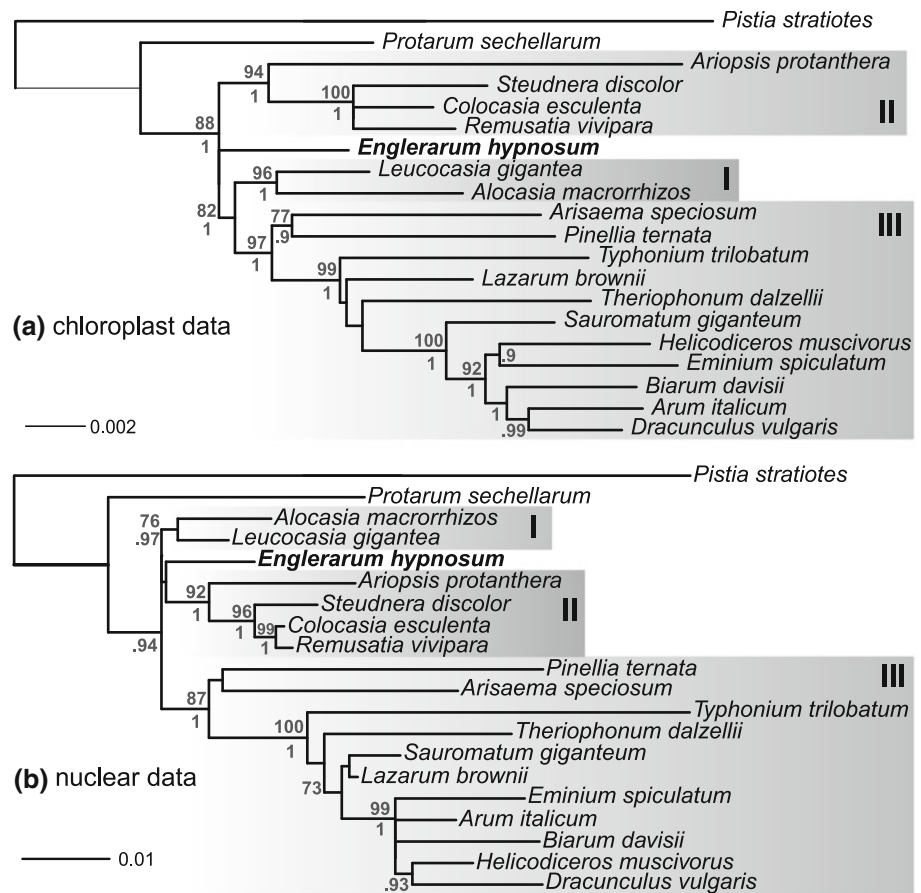
## Results

### Alignment

The aligned *trnL* sequences comprised 728 positions, of which we excluded 260 of one poly-T run, two poly-A runs, and a TA tandem array region. The *trnL-F* alignment comprised 439 nucleotides of which one poly-T run with five nucleotides was excluded. The length of the *rpl20-rps12* alignment was 807 nucleotides of which we

excluded 21 nucleotides of two poly-A runs and one poly-T run. The *trnK/matK* alignment included no ambiguously aligned sections, and was used in its entire length of 2,504 aligned positions. The combined chloroplast matrix included 4,178 base pairs. The alignment of the nuclear low-copy gene *phyC* comprised 1,074 nucleotides. The multistate matrix of the chloroplast data based on gap positions and indels proposed by SeqState contained 90 coded sites, of which six were informative and unambiguous.

**Fig. 2** Phylogenies of the *Pistia*-clade based on chloroplast data (a) and nuclear data (b). Statistical support is shown by node numbers; numbers above the stem lineage show bootstrap values (BS), underneath the stem lineage show posterior probabilities (PP) of respective nodes. Only BS of 70 or higher and PP of 0.9 or higher are displayed. Scale bars show substitutions per site. Roman numbers in shaded boxes mark the main clades: (I) *Alocasia*-clade (II) *Colocasia*-clade, and (III) Areae-clade



## Phylogenetic analyses

The analysis of the chloroplast dataset including gap positions and indels showed only small differences in support values, but did not change the topology of supported clades (Figure S1). In the following discussion only the analyses without gap coding are regarded.

All major clades (I) *Alocasia*- (II) *Colocasia*-, and the (III) Areae-clade, show moderate to high support, but almost all relationships between the clades remain unresolved (Fig. 2). Only the chloroplast phylogeny (Fig. 2a) shows support for a sister relationship of the *Alocasia*-clade and the Areae-clade (BS = 82, PP = 1), a relationship, which is not supported by the nuclear data (Fig. 2b). A comparison of the topologies of nuclear and chloroplast phylogenies revealed almost no disagreements of supported clades in the major groups of the *Pistia*-clade besides for the relationship of *Arum*, *Dracunculus*, *Eminium*, and *Helicodicerus* in the Areae tribe (III). In the chloroplast phylogeny, *Dracunculus* is sister to *Arum* (PP = 0.99) and *Helicodicerus* to *Eminium* (PP = 0.9), while in the nuclear phylogeny *Dracunculus* is sister to *Helicodicerus* (PP = 0.93). Because of this but also since major topological contradictions, possibly due to hybridization and chloroplast capture, were obtained within the genus

*Alocasia* in Nauheimer et al. (2012a), we opt for not combining nuclear with plastid data in this study. *Englerarum hypnosum* did not group with any of the three major clades, but remains isolated. Its relationship to the other main clades could not be resolved.

## Discussion

The finding that *Englerarum hypnosum* does not group with other *Alocasia* species, but represents an isolated lineage in the *Pistia*-clade standing next to the *Colocasia*-clade, the *Alocasia*-clade and the Areae-clade, revives discussion of the evolution of those lineages. Heinrich Gustav Adolf Engler (1876) was the first to put the genera of the subfamily Colocasioideae, which have anastomosing laticifers and colocasioid venation, into an evolutionary context. The taxonomic concept is based on the tribe Caladieae of Schott (1860), who focused on floral characters and includes a wider range of genera. Both Schott and Engler included the Neotropical genera *Caladium* Vent. and *Xanthosoma* Schott in the Colocasioideae, but despite being morphologically similar to the Asian genera, *Caladium* and *Xanthosoma* have been found to be not closely related to the Paleotropical members of Colocasioideae



(Colocasieae, sensu Mayo et al. 1997) based on molecular analyses (Cabrera et al. 2008; Cusimano et al. 2011). Phylogenies based on plastid data further showed that the Colocasieae is not monophyletic but includes the Arisaemateae and Areae as sister clade to *Alocasia* and *Leucocasia* with strong support (Renner and Zhang 2004; Cabrera et al. 2008; Cusimano et al. 2011). The inclusion of *Englerarum hypnosum* into the chloroplast dataset decreased this support, and its inclusion in the nuclear phylogeny even resulted into a monophyletic Colocasieae, although without any support (Fig. 2b). This potential contradiction has to be taken with care, as it is based on only one nuclear marker, the low-copy gene *phyC*. The inclusion of additional nuclear data will be needed to either strengthen or challenge the claim of a non-monophyletic Colocasieae. Nauheimer et al. (2012a) and the results of this study show the importance of sampling coverage, as the inclusion of *Englerarum hypnosum* obfuscated the previously supported relationship between the major clades of the *Pistia*-clade.

Further evidence for the isolated position of *Englerarum hypnosum* is provided by recent counts of chromosome numbers, which resulted in a haploid chromosome number  $n = 12$  (Aretuza Sousa dos Santos, pers. comm., August 2013, counted on voucher J. Bogner 3009 (M)). This is exceptional and stands in contrast to the haploid chromosome number  $n = 14$ , which is consistent across all closely related genera, *Ariopsis*, *Colocasia*, *Remusatia*, *Stuednera*, *Leucocasia*, and *Alocasia*, the more basal genera *Pistia*, *Protarum*, as well as *Pinellia*, *Arisaema*, and most genera of the Areae-clade. In addition, Cusimano et al. (2012) inferred a haploid chromosome number of  $n = 14$  for all ancestors of those lineages, although they do not include *Leucocasia* and *Englerarum* in their reconstruction. This may indicate the reduction of the chromosome number happened along the evolution of the lineage leading to *Englerarum*.

The age estimates of the molecular clock analysis of Nauheimer et al. (2012b) put the evolution of *Englerarum* into a temporal context. According to that study, the earliest most common ancestor of the *Pistia*-clade lived in the early Eocene at approximately 47 Ma ago [37–57 Ma, 95 % highest posterior density intervals (HPD)]. The *Colocasia*-clade, *Englerarum*, and the *Alocasia*-clade then evolved within a relatively short period from about 38 Ma (30–46 Ma, 95 % HPD) until the divergence of the Areae-clade at approximately 35 Ma ago in the end of the Eocene. It can be suggested, that the ancestor of the Colocasieae-grade resembled the morphology of *Alocasia*, *Englerarum*, and *Colocasia*, from which later diverging lineages show deviations, e.g., *Remusatia*, *Stuednera*, *Ariopsis*, and the ancestor of the Areae and Arisaemateae. This is supported by the fossil *Caladiosoma messelense* Wilde, Kvaček & Bogner from the Eocene of Messel, Germany (Wilde et al.

2005), which shows clearly the colocasioid venation and is most similar to *Alocasia* and *Colocasia*.

The findings of Nauheimer et al. (2012a), the exclusion of *Englerarum hypnosum* from *Alocasia* and the sister relationship of *Leucocasia* and *Alocasia*, alter the way *Alocasia* and *Colocasia* had been distinguished morphologically. Those two genera have a very similar morphology and have formerly been separated based on the type of placentation, fruit type, and synflorescence structure; *Colocasia* species have numerous fruit-smelling small berries, with many seeds and parietal placentation, and have been at least on one occasion been observed to be mammal dispersed (Hambali 1979), while *Alocasia* species produce rather few big scarlet or deep orange odorless berries each with large few seeds with a basal placentation, and seem adapted to bird dispersal, although reported observation is wanting (Hay 1998). However, based on the results of our molecular analyses, these characters are homoplastic. *Leucocasia gigantea* Schott (formerly assigned to *Colocasia*), although forming a clade with *Alocasia*, has parietal placentation with numerous ovules, and small pale brownish berries fragrant of decomposing pineapple, similar to *Colocasia* species. On the other hand, *Englerarum hypnosum* does not form a clade with *Alocasia* despite of a similar basal placentation and infructescences consisting of few, large scarlet berries. Thus, although these characters might be useful in the field, they cannot not be used for distinguishing those genera.

Recent observations from Sop Moei, Mae Hong Son, Thailand (J. Mood, pers. comm.) have revealed inflorescences of *Englerarum* to be heavily attended by Staphylinidae (Coleoptera), with in the population seen, seemingly a single staphylinid species responsible (Fig. 1d). Beetle pollination in *Alocasia* yet to be confirmed, with only a single reference (Shaw and Cantrell 1983) to beetles and where known all other studies showing *Alocasia* species to be pollinated by *Colocasiomyia* (Diptera: Drosophilidae). Although exhaustive observation has yet to be made, it would appear that staphylinid pollination is another taxonomically significant difference for *Englerarum* compared with *Alocasia*.

***Englerarum*** Nauheimer & P.C. Boyce, gen. nov.—Typus: *Englerarum hypnosum* (J.T.Yin, Y.H.Wang & Z.F.Xu) Nauheimer & P.C.Boyce, comb. nov.

Diagnosis: *Englerarum* is defined by the combination of leaf blades abaxially without waxy glands in the axils of the primary veins, a tuberous stem with a seasonally replaced active module, fully deciduous habit, and a protracted dormant period, and a colonial habit facilitated by the presence of much-elongated tubercle-tipped cataphyllary stolons, bimodular inflorescences arising tangentially to the stem, stamens grouped in synandria, a sterile appendix clothed with synandrodes, a persistent lower

spathe separated from a deciduous spathe limb by a single constriction, ovaries with basal placentation, an infructescence on an erect peduncle, comparatively large odorless fruits ripening scarlet and exposed by basiscopical spitting of the persistent lower spathe, and large seeds. *Englerarum* most closely resembles the genus *Alocasia* (Schott) G. Don but is differentiated by the leaf blades abaxially lacking waxy glands in the axils of the primary veins, a fully deciduous habit with a protracted dormant period, and the presence of much-elongated tubercle-tipped stolons.

Lithophytic or terrestrial seasonally dormant herbs. Stem compressed-globular tuberous, very seldom an erect rhizome-like tuber, active module replaced seasonally, when active producing from the upper surface numerous trailing or pendent cataphyllary stolons tipped with solitary tubercles. Leaves 3–6 per plant. Petiole terete, sheathing in the lower 1/2–1/3, sheath membranous, persistent; leaf blade triangular-sagittate, with basal lobes naked in the sinus; primary lateral veins pinnate, conspicuous; interprimary veins forming a feeble collecting vein, waxy glands absent. Inflorescences 2–3 together, appearing with leaves. Peduncle cylindrical. Spathe strongly constricted between lower convolute persistent part and deciduous limb; lower spathe fusiform; spathe limb oblong-lanceolate, fornicate, abruptly subtruncate at the junction with the lower spathe, erect at staminate anthesis, later flopping forwards, still later deliquescent. Spadix sessile, shorter than spathe; pistillate flower zone cylindrical; ovaries oblong. Style short, stigma 3–4 lobed; sterile interstice cylindrical; synandrodies depressed, apex nearly truncate or concave, oblong to ovate; staminate flower zone cylindrical synandria 5–6 merous, truncate; appendix well-developed, elongate-conic. Infructescence on an extended peduncle, erect. Fruiting spathe ellipsoid, splitting basiscopically to reveal the fruits when mature. Fruits ellipsoid berries, ripening scarlet. Seeds few per berry, comparatively large, globose, testa leathery.

**Distribution:** Continental tropical and subtropical southeast Asia, currently known from SW China (SW Yunnan), the Lao PDR, N & SW Thailand. Its presence in E Burma and NW Vietnam is to be expected.

**Habitat:** Humid ledges in exposed areas of forest regrowth and deciduous, bamboo-dominated forest on karst limestone; altitude: 800–970 m.

**Etymology:** The generic name honors Heinrich Gustav Adolf Engler (1844–1930), a German botanist who described many taxa and produced important monographs of the Araceae family. He provided a classification of the Araceae family based on anatomy and shoot organization, and was the first who regarded the phylogenetic relationship between the subfamilies.

***Englerarum hypnosum*** (J.T. Yin, Y.H. Wang & Z.F. Xu) Nauheimer & P.C. Boyce, comb. nov. Basionym: *A. hypnosa* J.T. Yin, Y.H. Wang & Z.F. Xu, Ann. Bot. Fenn. 42(5):

395 (–398; fig. 1). 2005. Type: China, Yunnan, Menglian County, by Nanlei River, limestone mountain margin, 975 m asl, 12 Aug. 2004 *Yin Jian-Tao 816* (holo HITBC).

Terrestrial or lithophytic seasonally dormant herbs up to 100 cm tall. Stem compressed-globular tuberous, very seldom an erect rhizome-like tuber with numerous stolons and tubercles; stem ca 10 × 13.5 cm diam.; stolons numerous per plant, simple, trailing horizontally or pendent, 56–110 cm long, pale green, internodes cylindrical, ca 5.5 cm long, to ca 1 cm diam., with light green cataphylls, and tubercles produced terminally; tubercles to 4 by 3 cm in diam., eventually detaching (by death of the stolon) and establishing as independent plants. Leaves 3–6 per plant. Petiole terete, up to 104 × 3 cm diam., glossy light green; petiolar sheath to ca half the length of the petiole, to 50 cm long, membranous, persistent; leaf blade triangular-sagittate, up to 82 × 64 cm but usually about half this size, membranous glossy bright green; basal lobes naked in the sinus; primary lateral veins pinnate, ca eight pairs per side, conspicuous; interprimary veins forming a feeble collecting vein. Inflorescences 2–3 together, appearing with the leaves. Peduncle cylindrical, to 90 cm long, pale green. Spathe up to 28 cm long, constricted between lower convolute part and limb; lower spathe fusiform, ca 6.5 × 3 cm diam., green, fleshy; limb oblong-lanceolate, to 24 × 20 cm (flattened), fornicate, purple-pink to bright pink, less often pale pink or white, erect at anthesis, later flopping forwards, then deliquescent. Spadix sessile, shorter than spathe; female flower zone cylindrical, 1.5 × 2 cm diam.; ovaries oblong, 5 mm long, style short, stigma 3–4 lobed; sterile interstice cylindrical, 5.5 by 1–1.5 cm diam.; synandrodies depressed, apex nearly truncate or concave, oblong to ovate, ca 2 × 2 mm; staminate flower zone cylindrical, ca 3.5 × 2 cm, white; synandria 5–6 merous, truncate, ca 2.5 × 2 mm; appendix white, elongate conic, to 16.5 cm long × 2.5 cm diam. Fruiting spathe ellipsoid, pale green, ca 3 × 2.5 cm. Berries ca 1.5 × 0.5 cm, green, ripening scarlet.

**Distribution:** SW China (Type), Thailand, Lao PDR.

**Habitat:** Humid ledges in exposed areas of forest regrowth and deciduous, bamboo-dominated forest on karst limestone; altitude: 800–970 m.

**Notes:** *Englerarum hypnosum* is a remarkable species, both in its vegetative habit (deciduous with long runners) and in the distinctive purple-pink spathe limb (Fig. 1c), although populations with a much paler, or even white, spathe limb have now been located. The long stolons enable the plants to colonize widely on the often vertical karst limestone outcrops that are their preferred habitat.

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## References

- Boyce PC, Wong SY (2008) Studies on Schismatoglottideae (Araceae) of Borneo VII: *Schottarum* and *Bakoa*, two new genera from Sarawak, Malaysian Borneo. *Bot Stud* 49:393–404
- Cabrera LI, Salazar GA, Chase MW, Mayo SJ, Bogner J, Davila P (2008) Phylogenetic relationships of aroids and duckweeds (Araceae) inferred from coding and noncoding plastid DNA. *Am J Bot* 95:1153–1165
- Cusimano N, Barrett MD, Hetterscheid WLA, Renner SS (2010) A phylogeny of the Aroideae (Araceae) implies that *Typhonium*, *Sauromatum*, and the Australian species of *Typhonium* are distinct clades. *Taxon* 59:439–447
- Cusimano N, Bogner J, Mayo SJ, Boyce PC, Wong SY, Hesse M, Hetterscheid WLA, Keating RC, French JC (2011) Relationships within the Araceae: comparison of morphological patterns with molecular phylogenies. *Am J Bot* 98:654–668
- Cusimano N, Sousa A, Renner S (2012) Maximum likelihood inference implies a high, not a low, ancestral haploid chromosome number in Araceae, with a critique of the bias introduced by 'x'. *Ann Bot* 109:681–692
- Engler A (1876) Vergleichende Untersuchungen über die morphologischen Verhältnisse der Araceae. I. Theil. Natürliches System der Araceae. *Nov. Acta Kaiserl. Leopold.- Carol.- Deutschen Akad. Naturforscher* 39:134–155
- Gonçalves EG (2005) Two new Andean genera for the tribe Spathicarpeae (Araceae). *Willdenowia* 35:319
- Gonçalves EG (2012) *Lorenzia* (Araceae - Spathicarpeae): a new genus from northern Brazil supported by matK sequence data. *Syst Bot* 37:48–52
- Hambali GG (1979) The dispersal of taro by common palm civets. In: International symposium trop root tuber crop—5th Symposium Proc 545–547
- Hay A (1998) The genus *Alocasia* (Araceae-Colocasiaceae) in West Malesia and Sulawesi. *Gard. Bull. Singapore* 50:221–334
- Mayo SJ, Bogner J, Boyce PC (1997) The Genera of Araceae. Royal Botanic Gardens, Kew
- Müller DK (2005) SeqState. *Appl Bioinformatics* 4:65–69
- Nauheimer L, Boyce PC, Renner SS (2012a) Giant taro and its relatives: A phylogeny of the large genus *Alocasia* (Araceae) sheds light on Miocene floristic exchange in the Malesian region. *Mol Phylogenet Evol*: 43–51
- Nauheimer L, Metzler D, Renner SS (2012b) Global history of the ancient monocot family Araceae inferred with models accounting for past continental positions and previous ranges based on fossils. *New Phyt* 195:938–950
- Renner S, Zhang L-B (2004) Biogeography of the *Pistia* Clade (Araceae): based on chloroplast and mitochondrial DNA sequences and Bayesian divergence time inference. *Syst Biol* 53:422–432
- Ronquist F, Huelsenbeck JP (2003) MrBayes 3: bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574
- Schott HW (1860) *Prodromus systematis Aroidearum*. Typis congregationis mechitharisticae, Vienna
- Shaw DE, Cantrell BK (1983) A study of the pollination of *Alocasia macrorrhiza* (L.) G. Don (Araceae) in southeast Queensland. *Proc Linn Soc N.S.W.* 106:323–335
- Silvestro D, Michalak I (2012) raxmlGUI: a graphical front-end for RAxML. *Org Divers Evol* 12:335–337
- Stamatakis A (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22:2688–2690
- Wang YH, Yin JT, Xu ZF (2005) *Alocasia hypnosa* (Araceae), a new species from Yunnan, China. *Ann Bot Fenn* 42:395–398
- Wilde V, Kvaček Z, Bogner J (2005) Fossil Leaves of the Araceae from the European Eocene and Notes on Other Aroid Fossils. *Int J Plant Sci* 166:157–183
- Wong SY, Boyce PC (2010a) Studies on Schismatoglottideae (Araceae) of Borneo IX: a new genus, *Hestia*, and resurrection of *Apoballis*. *Bot Stud* 51:249–255
- Wong SY, Boyce PC (2010b) Studies on Schismatoglottideae (Araceae) of Borneo X. *Pichinia*, a new genus from Sarawak, Malaysian Borneo. *Gard Bull Singapore* 61:541–548
- Wong SY, Boyce PC (2010c) Studies on Schismatoglottideae (Araceae) of Borneo XI: *Ooia*, a new genus, and a new generic delimitation for *Piptospatha*. *Bot Stud* 51:543–552