

Hayarum mirispathum (Araceae — Aroideae): A new genus and species from Thailand

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ABSTRACT: The new monotypic genus *Hayarum* K.Z.Hein, Prehsler, Saensouk & S.L.Low from Thailand, with the sole species *Hayarum mirispathum* K.Z.Hein, Prehsler, Saensouk & S.L.Low, is described based on comprehensive morphological and phylogenetic evidence. A detailed taxonomic account of the new genus, morphological comparisons with related genera, and brief observations on its flowering biology and spathe movement are provided.

KEY WORDS: Areae, Arisaemateae, Indochina, insect-trapping mechanism, Pinellia, spathe movement, Typhonium.

INTRODUCTION

The family Araceae Juss. is the third largest family of monocots, consisting of 144 genera and an estimated 8,110 species worldwide, of which about 3,676 are formally described (Boyce and Croat, 2011; Croat and Ortiz, 2020). The increase in accepted genera within Araceae, from 105 (Mayo et al., 1997) to 144 (Boyce and Croat, 2011), is partly due to the merging of the former family Lemnaceae, which includes five genera, into Araceae as the subfamily Lemnoideae (Cabrera et al., 2008). Additionally, many molecular phylogenetic studies, combined with extensive fieldwork in the humid tropics have shown the non-monophyly of previously described genera, leading to the reclassification of several groups (e.g., Gonçalves et al., 2007; Cabrera et al., 2008; Wong et al., 2010; Cusimano et al., 2011; Low et al., 2018; Abdullah et al., 2020; Haigh et al., 2023). Consequently, some species from previously poorly studied and inadequately known genera have been reclassified into new genera (e.g., Gonçalves, 2005; Boyce and Wong, 2008; Wong and Boyce, 2010a; Nauheimer and Boyce, 2013; Low et al., 2018) or resurrected as separate genera (e.g., Wong and Boyce, 2010b; Wong et al., 2010, 2016; Low et al., 2013; 2018, Hay et al., 2022; Hay, 2023). Furthermore, the discovery of entirely new genera based on new collections has contributed to this increase, including Schottariella P.C.Boyce & S.Y.Wong (Boyce and Wong, 2009), Pichinia S.Y.Wong & P.C.Boyce (Wong and Boyce, 2010c), Lorenzia E.G.Gonç. (Gonçalves, 2012), Fenestratarum P.C.Boyce & S.Y.Wong (Boyce and Wong, 2014), Galantharum P.C.Boyce & S.Y.Wong (Boyce and Wong, 2015), Vietnamocasia N.S.Lý, S.Y.Wong & P.C.Boyce (Lý et al., 2017), Bidayuha S.Y.Wong & P.C.Boyce (Low et al., 2018), Idimanthus

E.G.Gonç. (Gonçalves, 2018), and *Josefia* Scherber., K.Hase & P.C.Boyce (Scherberich *et al.*, 2023).

The tribe Areae (sensu Mayo et al., 1997, see also Cusimano et al., 2010, 2011; Nauheimer et al., 2012) comprises nine genera of seasonally dormant geophytes, with an estimated 208 species, of which approximately 173 are formally described (Boyce and Croat, 2011). Areae is one of the most widespread tribes in Araceae, ranging from the Azores, Ireland, and Sweden through to tropical and warm temperate Australia (Hay and Hein, 2022). Within this tribe, the limits and definitions of the Mediterranean-focused (though some are more widespread) temperate and warm temperate genera-Arum L., Biarum Schott, Dracunculus Mill., Eminium (Bl.) Schott, and Helicodiceros Schott ex K.Koch-have remained relatively stable despite molecular-systematic upheavals within the family (Cusimano et al., 2010, 2011; Nauheimer et al., 2012). However, the generic boundaries of the Palaeotropical and Australian genera (excluding Theriophonum Schott) -Lazarum A. Hay, Sauromatum Schott, and Typhonium Schott, have been particularly problematic to define morphologically. Pre-molecular perspectives varied on whether Lazarum and Sauromatum should be distinguished from Typhonium (e.g., Hay, 1992, 1997; Hetterscheid and Boyce, 2000; Sriboonma et al., 1994). Cusimano et al., (2010) resolved phylogenetic relationships within the tribe Areae using nuclear and chloroplast genes, showing that Typhonium sensu lato was polyphyletic. They concluded that to avoid Typhonium being polyphyletic, the Australian and some Asian species must be excluded from Typhonium sensu lato. Cusimano et al., (2010) transferred these Asian species to Sauromatum, but the Australian species were retained in Typhonium pro tempore, as the type species of Lazarum, L. mirabile, had not yet been sequenced and its position remained uncertain due to the absence of morphological synapomorphies for the Australian clade. Recently, the transfer of Australian species to *Lazarum* was completed by Hay *et al.*, (2022), after confirming that the type species of *Lazarum* is phylogenetically deeply embedded within the Australian clade.

The sister tribe of Areae, Arisaemateae Nakai (sensu Mayo *et al.*, 1997) includes two genera of evergreen or seasonally dormant geophytes—*Arisaema* Mart., a widespread genus with approximately 200 species distributed from Northeast Africa to the tropical, subtropical, and temperate regions of East Asia and North America (Ohi-Toma *et al.*, 2016); and *Pinellia* Ten., a genus with about ten species found primarily in China, Korea, and Japan (Zhu *et al.*, 2007). Although molecular techniques, particularly mitochondrial and chloroplast DNA analyses, indicate that *Pinellia* and *Arisaema* are closely related to the tribe Areae, their precise relationships remain unresolved (Renner *et al.*, 2004; Renner and Zhang 2004; Cusimano *et al.*, 2011; Nauheimer *et al.*, 2012).

The late Alan Galloway's collection of unusual tuberous aroids includes an intriguing specimen labeled Typhonium sp. #114 (AGA-2613-01), originally collected in Loei Province, Northeastern Thailand. Images of this enigmatic plant are available on Alan Galloway's Botanical Website [http://alangallowaybotanicals.com/plants/aroids/typhoni um/un/sp-114/], a valuable resource for geophytic aroids, especially Amorphophallus and Typhonium species. Since its discovery, this taxon has remained undescribed, known only by its accession number. Tubers from the same province were later received and cultivated by the first author (KZH) and second author (DP). The morphology of the inflorescence and the flowering biology of this taxon are unusual for Typhonium, prompting DNA sequencing and analysis to determine its phylogenetic position within the genus. Molecular analysis revealed that this taxon is not related to either Typhonium or Sauromatum. Thus, we propose that Typhonium sp. #114 (AGA-2613-01) represents not only an undescribed species but also a new genus, which we describe in detail here.

MATERIAL AND METHODS

Morphological and flowering biological observations

Measurements and morphological descriptions were based on fresh materials and spirit-preserved specimens. Terminology for spathe morphology follows Hetterscheid and Boyce (2000), where the spathe base refers to the basal part of spathe formed by the convolute margins, the spathe limb refers to the upper, expanded part, and both are separated by a constriction. Observations of flowering biology were conducted from July to August 2024 to confirm pistillate and staminate stages of anthesis. These observations were based on five inflorescences from living specimens cultivated at the Botanical Garden of the University of Vienna, Austria. Voucher specimens have been deposited in the WU and L herbarium collection (see Taxonomic Treatment section).

DNA isolation and Illumina sequencing

Silica gel-dried leaf sample was outsourced to the Beijing Genomic Institute (BGI) for DNA isolation, and a 5G paired-end (PE) sequencing library was constructed, targeting DNA fragments between 300-350 bp in length. The library preparation followed the protocol described by Low *et al.* (2020), however the clustered flow cell was loaded onto a HiSeq X10 sequencer (Illumina Inc., USA) for PE sequencing.

Plastome assembly

Plastome assembly from the 5G of raw sequencing data was performed on the Metacentrum computational infrastructure (CESNET, Czech Republic) using GetOrganelle ver.1.7.6.1 (Jin *et al.*, 2020), with dependencies including SPAdes (Prjibelski *et al.*, 2020), Bowtie2 (Langmead and Salzberg, 2012), BLAST+ (Camacho *et al.*, 2009), and Bandage (Wick *et al.*, 2015). The assembled plastome genome was annotated using GeSeq available on Chlorobox platform (Tillich *et al.*, 2017). Annotated sequences were deposited to NCBI under the accession number PQ772791.

Plastome alignment and phylogenetic analyses

To determine the phylogenetic placement whether the studied species belongs to Typhonium, the assembled entire plastome was concatenated with 67 plastome sequences from the tribes Areae, Arisaemateae, and Colocasieae (Low et al., 2020; Table S1). Three additional plastome sequences representing the genus Arum and Dracunculus (Low and Landrein, in prep.) were included in the dataset. The sequences were aligned using MAFFT-7.453 (Katoh and Standley, 2013), and complementary orientations of plastome were replaced using the second available plastome sequence from GetOrganelle. A maximum likelihood (ML) tree was constructed using IQtree2 (Minh et al., 2020), and Bayesian inference (BI) analysis was performed using BEAST v.2.7.1 (Bouckaert et al., 2019) for 100 000 000 generations. A general time reversible (GTR) substitution rate model based on model selection results and relaxed log normal clock model were applied. All computations were performed on the Metacentrum infrastructure. Distribution trees generated from BEAST were assessed for the effective sample size (ESS) of parameters and convergence using Tracer (Rambaut et al., 2018); and the first 10% were discarded as burn-in using LogCombiner (Drummond and Rambaut, 2007). The final maximum clade credibility (MCC) tree was summarized using TreeAnnotator (Drummond and Rambaut, 2007).



RESULTS

Phylogenomic analyses

In line with the sequences from Low *et al.*, (2020), the targeted assembled sequence in this study spanned over 160 000 bases. The entire dataset including 71 accessions, contained 224 218 aligned bases. Phylogenomic analyses yielded identical strongly supported tree topologies for both ML and BI, with high bootstrap support (BS > 90) and posterior probabilities (PP= 0.9-1.0). Our results indicated that the taxon studied does not belong to *Typhonium* or the tribe Areae. However, it is strongly supported (BS = 100) as a lineage that branched-off before *Pinellia ternata* (Fig. 1), or is embedded between *P. ternata* and *Arisaema prazeri* (PP= 0.9962) (Fig. 2).

Additionally, based on flowering observations from cultivated specimens and detailed morphological diagnosis, the taxon exhibited unique traits, including spathe movement (Fig. 3B–E) and by having a unilocular ovary with a sessile ovule (Fig. 3G), which align with the characteristics of the genus *Pinellia*. However, due to other distinguishing features that deviate from *Pinellia*, we propose the establishment of a new genus – *Hayarum* K.Z.Hein, Prehsler, Saensouk & S.L.Low.

TAXONOMIC TREATMENTS

Hayarum K.Z.Hein, Prehsler, Saensouk & S.L.Low, gen. nov.

Diagnosis: Hayarum, with its sole species H. mirispathum, is uniquely defined by the combination of its remarkable spathe movement during anthesis, a pistillate zone of the spadix free from the spathe, a short sterile zone between the pistillate and staminate zones which is completely covered with a single whorl of subglobose staminodes, a staminate zone wholly contained within the spathe base and a unilocular ovary with a single erect, sessile ovule on a basal placenta. Hayarum shares certain morphological features with the genus Pinellia, notably the unilocular ovary with a single erect, sessile ovule on a basal placenta, and the gaping of spathe base margins during late staminate anthesis. However, in Pinellia, the spathe is mostly with a transverse septum between the pistillate and staminate zone, and its pistillate zone is adnate to the spathe. In contrast, Hayarum lacks this transverse septum and its pistillate zone is entirely free from the spathe. The inflorescence of Hayarum resembles that of the genus Typhonium, but the latter differs by having non-opening spathe base throughout anthesis, ovaries with a single ovule held obliquely on a funicle on a basal placenta, and a staminate zone which is completely exserted from the spathe base.

Type species: Hayarum mirispathum K.Z.Hein, Prehsler, Saensouk & S.L.Low.

Description: Small, deciduous, perennial herb. Stem a hypogeal, depressed globose tuber. Leaves 1-4 together; petiole erect or weakly arching, slender, glabrous, terete proximally, weakly D-shaped in cross section distally; petiolar sheath ca. 1/4 of petiole length; leaf blade ovate broadly ovate-cordate; primary lateral veins to anastomosing and terminating in an intramarginal collective vein; higher order venation reticulate. Inflorescence solitary, appearing together with the leaves, emitting a scent reminiscent of pear or green apple at pistillate anthesis, subtended by a cataphyll; peduncle terete, glabrous, green; spathe strongly differentiated into a convolute spathe base and a spathe limb, both separated by a constriction opposite the base of the appendix; spathe base cylindric, margins free, convolute during both pistillate and staminate anthesis, then widely gaping to reveal the staminate zone at late staminate anthesis with margins recurving; spathe limb lanceolate, strongly reflexed and curled during pistillate anthesis, then becoming erect and expanding at staminate anthesis, and later closing, partly leaving the appendix visible at late staminate anthesis with margins curved inwards. Spadix shorter than spathe, sessile, divided into five distinct zones from the base upwards—namely (i) pistillate zone, (ii) sterile zone, (iii) staminate zone, (iv) supra-staminal sterile zone and (v) appendix. Pistillate zone shortly subcylindric; ovary obovoid, angular or subangular in cross section, unilocular with a single erect, sessile ovule on a basal placenta, with at most a small apical void between the ovule and the locule wall; style prominent, conical, curved outwards and slightly downwards; stigma discoid, papillate; sterile zone between pistillate and staminate zones very short, completely covered with a single whorl of staminodes; staminate zone wholly contained within the spathe base, subcylindric or subconical; staminate flowers each consisting of 1 stamen; stamens free, slightly distant, butterfly-shaped from above, each with 2 anthers; anthers subsessile, each with 2 thecae; thecae dehiscing by apical pore; supra-staminal sterile zone lower part naked and smooth, upper part covered with a single whorl of fused staminodes; appendix stipitate, narrowly oblongclavate, erect, glabrous.

Etymology: The generic name Hayarum honors British botanist Alistair Hay (+ 'arum', from the Greek apov, an ancient name for Arum). Alistair Hay is an expert on Asian Araceae and the former Director of the Sydney Botanical Garden in Australia. In recognition of his outstanding contributions to aroid research, he was awarded the H.C. Schott Award for excellence in aroid research in 2023. Hay is regarded as the world authority on the subfamily Lasioideae (Araceae) and has conducted extensive research on the Malesian and Australian Araceae. He also inspired the first author (KZH) to pursue the study of aroids and has always kindly suggested and guided throughout his aroid research.





Fig. 1. Maximum likelihood (ML) tree generated using IQtree2. Numbers on nodes represented the bootstrap support (BS). 68





Fig. 2. Bayesian inference generated using BEAST2. Numbers on nodes represented the posterior probability (PP).

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Hayarum mirispathum K.Z.Hein, Prehsler, Saensouk & S.L.Low, sp. nov. Fig. 3

Type: Cultivated at Botanical Garden of the University of Vienna, Austria, 30 July 2024, *D. Prehsler HBV-WU00034323* (original collection: THAILAND (Northeastern), Loei province, *A. Galloway's collection AGA-2613-01*) (holotype: WU, isotypes: WU, L, spirit collection).

Diagnosis: Hayarum mirispathum bears the closest morphological resemblance to Pinellia and Typhonium. Hayarum mirispathum differs from Pinellia in several key morphological traits. It has a pistillate zone of the spadix that is free from the spathe, a short sterile zone between the pistillate and staminate zones that is completely covered with a single whorl of staminodes, and a spadix shorter than the spathe. In contrast, Pinellia exhibits a pistillate zone adnate to the spathe, a longer prominent sterile zone between the pistillate and staminate zones that is entirely naked, and a spadix much longer than the spathe. Hayarum mirispathum differs from Typhonium, to which it bears the closest resemblance, in having gaping spathe base margins during late staminate anthesis, a unilocular ovary with a single erect, sessile ovule on a basal placenta, and a staminate zone that is fully contained within the spathe base. Typhonium possess non-gaping spathe base margins throughout anthesis, a unilocular ovary with a single obliquely positioned ovule on a funicle on a basal placenta, and a staminate zone fully exserted from the spathe base.

Description: Small, tuberous, deciduous, perennial herb to 15 cm tall. Stem a hypogeal, depressed globose tuber, 2.2-2.7 cm in diameter, pale brown outside, white inside. *Roots* filiform, flexuous, 1.0-1.2 mm in diameter, white. Leaves 1-4 together; petioles erect or weakly arching, 5.0-10.5 cm long, 3.0-3.5 mm in diameter, slender, glabrous, pale green, terete proximally, weakly D-shaped in cross section (dorsally shallowly grooved) distally; petiolar sheath 1.3-2.5 cm long, ca. 1/4 of petiole length; *leaf blade* ovate to broadly ovate-cordate, 5.5-12.0 cm long, 3.5-8.0 cm wide, thinly coriaceous, glabrous on both sides, adaxially glaucous green or medium green, abaxially pale green, margin entire; anterior lobe apex attenuate or acuminate; posterior lobes pointing downwards, 1/8-1/5 the length of the anterior lobe, apexes rounded, sinus between posterior lobes acute; *midrib* impressed adaxially, rounded raised abaxially, 3.0-3.5 mm wide at the base, ca. 0.2 mm wide at center, then narrowing towards blade apex; primary lateral veins impressed adaxially, raised abaxially, 7-8 per side, diverging from the midrib at 30-55°, anastomosing and terminating in an intramarginal collective vein at 3.0-5.0 mm from margin; higher order venation reticulate. Inflorescence solitary, emitting a scent reminiscent of pear or green apple at pistillate anthesis, subtended by a cataphyll; peduncle 6.0-10.0 cm long, 2.5-3.0 mm in

diameter, terete, glabrous, green; spathe 7.7-8.3 cm long, strongly differentiated into a convolute spathe base and a spathe limb, both separated by a constriction opposite the base of the appendix; spathe base cylindric, 2.0-2.2 cm long, ca. 0.7 cm in diameter, slightly truncate at base, coriaceous, glabrous, externally pale green with darker green veins, internally pale green, margins free, convolute during both pistillate and staminate anthesis, then widely gaping to revel the staminate zone at late staminate anthesis with margins recurving; spathe limb lanceolate, 5.7-6.1 cm long, 1.4-1.8 cm wide at widest point, coriaceous, glabrous, externally pale green with darker green veins, internally greenish or yellowish glaucous white, apex attenuate with convolute margins remaining furled, spathe limb strongly reflexed and curled during pistillate anthesis, then becoming erect and expanding at staminate anthesis, and later closing, partly leaving the appendix visible at late staminate anthesis with margins curved inwards. Spadix shorter than spathe, 5.3-6.0 cm long, sessile; pistillate zone shortly subcylindric, 2.0-2.5 mm long, 3.5-4.0 mm in diameter, with 3 whorls of congested pistils; ovary obovoid, angular or subangular in cross section, 0.7-0.8 mm high, 0.8-1.0 mm in diameter, medium green, unilocular with a single erect, sessile ovule on a basal placenta, with at most a small apical void between the ovule and the locule wall; style prominent, conical, 0.5-0.7 mm high, 0.3-0.4 mm in diameter at base, ca. 0.2 mm in diameter at apex, curved outwards and slightly downwards, medium green; stigma discoid, ca. 0.3 mm in diameter, white, papillate; sterile zone between pistillate and staminate zones very short, 1.1-1.3 mm long, 2.5-3.0 mm in diameter, completely covered with a single whorl of more or less loosely arranged staminodes; staminodes free, slightly distant, globose or sub-globose, 0.7-0.8 mm long, 0.6-0.8 mm in diameter at widest point, glabrous, orange; staminate zone wholly contained within the spathe base, subcylindric or subconical, 4.0–5.8 mm long, 3.0–3.8 mm in diameter; staminate flowers each consisting of 1 stamen; stamens free, slightly distant, butterfly-shaped from above, 0.6–1.0 mm in diameter, yellow, each with 2 anthers; anthers subsessile, each with 2 thecae; thecae dehiscing by apical pore; supra-staminal sterile zone 3.5-4.0 mm long, lower ca. 2 mm naked, purple, upper 1.5-2.2 cm covered with a single whorl of fused staminodes; staminodes conical or pyramidal, basally or entirely connate to neighboring staminodes, slightly curved outwards or downwards, 1.2-1.3 mm high, 0.8-0.9 mm wide at base, glabrous, purple; appendix stipitate, narrowly oblong-clavate, 4.2-4.3 cm long including stipe, 3.6-4.0 mm in diameter at widest point, erect, glabrous, cream or orange, base slightly attenuate, apex obtuse; stipe cylindric, 0.5-0.6 cm long, 1.2-1.5 mm in diameter, white. *Infructescence* not seen.

Distribution and habitat: Hayarum mirispathum, is currently known only from Loei province in northeastern





Fig. 3. *Hayarum mirispathum* gen. nov. et. sp. nov. **A.** Cultivated flowering plant, **B.** Inflorescence at pistillate anthesis (spathe limb strongly reflexed and curled), **C.–D.** Inflorescence at post pistillate anthesis (spathe limb beginning to uncurl and gradually becoming erect), **E.** Inflorescence at post staminate anthesis (pollen released, spathe limb closing, partly leaving the appendix visible and remaining erect, spathe base margins recurve and gaping, revealing the staminate zone), **F.** Detail of spadix showing pistillate zone, sterile zone, staminate zone, supra-staminal sterile zone, and base of the appendix (nearside spathe artificially removed), G. Longitudinal section of pistil with with a single erect, sessile ovule on a basal placenta. Scale bars: A=2 cm, B–E=1 cm, F=5 mm. Photos by D. Prehsler.



Thailand. The species inhabits shaded to semi-shaded environments, thriving within the crevices of limestone mountains.

Phenology: Observed flowering in July and August – in cultivation at the Botanical Garden of the University of Vienna, Austria.

Etymology: The specific epithet *mirispathum* is derived from the Latin '*mirus*' (wonderful or marvelous) and '*spathus*' (spathe) referring to the remarkable spathe movement observed during anthesis in this species.

Provisional conservation status: This new species is known only from its type locality and requires further observation to determine if other populations exist in neighboring areas. Due to insufficient data on its distribution and population size, we herein proposed it to be classified as 'Data Deficient' (DD) according to IUCN Red List criteria (IUCN Standards and Petitions Subcommittee, 2024). However, this classification does not rule out the possibility that the species is not threatened as additional surveys are necessary to ascertain its conservation status.

Additional specimen examined (paratypes): Cultivated at Bangkok, 16 July 2024, Siddharath Saigal s.n. (original collection: THAILAND, Loei province) (TTM, spirit collection); Cultivated at Yala, 17 August 2024, Apisit Kangjanataworn s.n. (original collection: THAILAND, Loei province) (TTM, spirit collection).

Brief observations on flowering biology and spathe movement: Hayarum mirispathum exhibits a protogynous flowering pattern, with pistillate anthesis beginning one day prior to staminate anthesis.

Day 1: The pistillate anthesis begins early in the morning, with a gap opening along the spathe limb, accompanied by the emission of a scent reminiscent of pear or green apple. During this time, the spathe limb reflexes and curls strongly (Fig. 3B). By late evening, the spathe limb starts to uncurl and gradually becomes erect (Fig. 3C), fully erecting and expanding throughout the night (Fig. 3D). The scent emission ceases at night, corresponding to the end of pistillate anthesis. The spathe base margins remain strongly convolute throughout the day and night (Fig. 3B–D).

Day 2: Staminate anthesis commences before dawn, with the release of powdery pollen. During this phase, the spathe limb remains erect, and then closing, partly leaving the appendix visible, with its margins rolling inwards, while the spathe base margins remains convolute. At late staminate anthesis, occurring early in the morning, the spathe base margins below the constriction begin to recurve and gape widely, revealing the staminate zone (Fig. 3E), while the spathe limb remains erect and continues closing, partly leaving the appendix visible. This gaping persists into the evening. As these observations were made on cultivated specimens, no pollinators visited the inflorescence, and it was not artificially pollinated. Consequently, the entire inflorescence began to wither on the following day.

Although Hayarum mirispathum has not been

observed in its natural habitat and the pollinator remains unknown, we hypothesize that the gaping of the spathe base margins during late staminate anthesis serves to release captured insects from the spathe base. This insecttrapping mechanism is consistent with the *Zomicarpa*type trap (sensu Bröderbauer *et al.*, 2012), where the spathe base margins are always convolute, completely hiding the fertile part of the spadix within the spathe base. Insects are trapped by the slippery surfaces of the spathe base margins open to form a secondary exit. This trapping mechanism is observed in two genera of the subfamily Lasioideae (viz. *Lasia* and *Dracontioides*), and three genera of Aroideae (viz. *Arisaema, Pinellia*, and *Zomicarpa*) (Bröderbauer *et al.*, 2012).

Taxonomic notes: Our molecular analyses, based on maximum likelihood (ML) support, support Havarum as a divergent lineage that precedes Pinellia, Arisaema, and the tribe Areae (Fig. 1). In contrast, Bayesian inference places Hayarum as sister to a (BI) clade containingPinellia and Arisaema (Fig. 2). Interestingly, the gaping of the spathe base margins during late staminate anthesis, observed in Arisaema and Pinellia (Vogel and Martens, 2000), is also seen in Hayarum. However, in Arisaema and Pinellia, the gaping of the spathe base is limited to a small opening at the base of the spathe base margins (Vogel and Martens, 2000), while in Hayarum, the spathe base margins gapes widely, exposing the staminate zone. Additionally, the duration of anthesis in Hayarum is much shorter, lasting approximately 24 hours, whereas in Arisaema and Pinellia, anthesis can last a week or even several weeks (Vogel and Martens, 2000). Within the genera of the tribe Areae, anthesis typically lasts 24 hours, but the spathe base margins remain strongly convolute or fused, lacking the wide gaping characteristic seen in Hayarum (Bröderbauer et al., 2012). One exception within the tribe Areae is Dacunculus canariensis Kunth, where the spathe base margins gape during anthesis, revealing the staminate zone (Boyce, 1994). While our molecular analyses provide conflicting placements for Hayarum, it is morphologically, Hayarum distinct from the genera of both the tribes Arisaemateae and Areae. We acknowledge that the phylogenetic relationships between Hayarum, Pinellia and Arisaema are not fully resolved, and additional molecular data, particularly for more species of Pinellia and Arisaema, would help clarify these relationships. Based on the current data, we propose that Hayarum, Pinellia, and Arisaema may form a grade, and further investigation is needed to clarify their evolutionary relationships.

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