PHYLOGENY AND EVOLUTIONARY HISTORY OF VIETNAMESE *Arisaema* (ARACEAE)

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SUMMARY

In the family Araceae, Arisaema Mart is one of the largest genera with 200 species in the world, and mainly distributed in the temperate and warm-temperate areas from the East to South-East of North America to northern Mexico, from tropical East and North-East Africa to the Arabian Penisula, and from temperate East Asia to South and South-East Asia and Malesia. Several species of Arisaema are used as food and local medicine in India, China and Vietnam. Exploring the relationship between plants and explaining where plants originated and how they migrated between regions in the world and Vietnam is still challenging. Construction of molecular phylogeny, estimations of the divergence time and ancestral area of lineages based on evidences of molecular data, fossils, geology have provided major insights into plant evolution. This study was conducted based on comprehensive taxon sampling and molecular data from four chloroplast DNA regions of *Arisaema* to determine the phylogeny and evolutionary history of Vietnamese *Arisaema* (Araceae). The phylogeny of *Arisaema* was studied by using ML and BI methods. Our results indicated that *Arisaema* originated in Southeast Asia at ca. 31 Ma during the Oligocene and that Vietnamese *Arisaema* was derived from the Southeast Asia *Arisaema* during climate optimum period of Mid-Miocene with the presence and development of the tropical rainforest. Whereas, Vietnamese *Arisaema* likely does not have any connection with *Arisaema* from India, North China, Japan and the Korean Peninsula regions.

Keywords: Arisaema, molecular data, phylogeny, Southeast Asia, Vietnam.

1. INTRODUCTION

Exploring the relationship between plants and explaining where plants originated and how they migrated between regions in the world is still challenging. Construction of molecular phylogeny, estimations of the divergence time and ancestral area of lineages based on evidences of molecular data, fossils, geology have provided major insights into plant evolution (Nauheimer *et al*., 2012).

In the family Araceae, *Arisaema* Mart. is one of the largest genera with ca. 200 species in the world (Ohi-Toma *et al*., 2016), and mainly distributed in the temperate and warm-temperate areas from the East to South-East of North America to northern Mexico, from tropical East and North-East Africa to the Arabian Penisula, and from temperate East Asia to South and South-East Asia and Malesia (Govaerts *et al*., 2002; Gusman & Gusman 2006; Murata 2011; Ohi-Toma *et al*., 2016). Several species of *Arisaema* are used as food and local medicine in India, China and Vietnam (Gusman & Gusman 2006; Li *et al*., 2010).

Since being established in 1831, there are many studies of *Arisaema* published on both classification system and phylogeny and several systems of classification proposed by Schott (1860), Engler (1920), Nakai (1950), Hara (1971), Murata (1984, 1991), Gusman & Gusman (2002, 2006), Li *et al*. (2010), Murata (2011), Murata *et al*. (2013) and Ohi-Toma *et al*. (2016). All of the above studies focused onsystematics and have provided a foundation for investigating the phylogeny and historical biogeography of the genus *Arisaema*.

Renner *et al*. (2004) conducted the first phylogenetic study based on 81 individuals of *Arisaema*. Results of this study supported the monophyly of this genus, but several polytomies were found in the phylogenetic trees of *Arisaema*. Additionally, the study also estimated the divergence time of the genus, provided the main biogeographical event of *Arisaema*, and considered floristic links among East Africa, Arabia, the Himalayan region, China, and North America. However, this study used only one calibration point (the fossil similar to *A. triphyllum* at 18 million years ago (Ma)) and penalized likelihood. The resulting time estimates are not sufficiently reliable to clarify the divergence time of

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Arisaema, and the biogeography of *Arisaema* was not discussed in detail.

In the previous botanical studies in Vietnam, the molecular phylogeny and historical biogeography analyses are limited, thus exploring the molecular relationship as well as the evolutionary history of plants is incomplete, in which *Arisaema* is an example. Even the flora of Vietnam on Araceae that was published by Nguyen Van Du (2017), however, the molecular phylogenetic relationship and evolutionary history of the Vietnamese *Arisaema* is still unclear.

In this study we report phylogenetic and biogeographical analyses based on molecular data from chloroplast DNA regions of 131 species of *Arisaema*. Our major aims are to (1) clarify the molecular phylogenetic relationship of Vietnamese *Arisaema*; (2) investigate the evolutionary history of Vietnamese *Arisaema* based on present day distributions, fossil data, and geological information of the genus.

2. RESEARCH METHODOLODY

2.1. Sampling, DNA extraction, amplification and sequencing

In total, our data were obtained from 131 species of *Arisaema* for all 15 sections of the genus. Thus, the molecular data in this study represents most geographical and taxonomic diversity in the genus with approximately 66% of *Arisaema* species.

For the two *Arisaema* samples from Vietnam, we extracted genomic DNA from silica gel dried leaves using the CTAB procedure (Doyle & Doyle 1987). Polymerase chain reactions and sequencing were performed using the primers presented in Ohi-Toma *et al.* (2016). PCR products were separated and visualized using an ABI3730 automated sequencer (Applied Biosystems, USA). Four chloroplast DNA regions (*trnL–trnF*, *rpl20–rps12*, *psbB–psbH* and *rps2–rpoC2*) were used in this study. The electrophoresis results of this study presented in Fig.1. All sequences were aligned in Geneious v.8.0.5 (Kearse *et al.*, 2012).

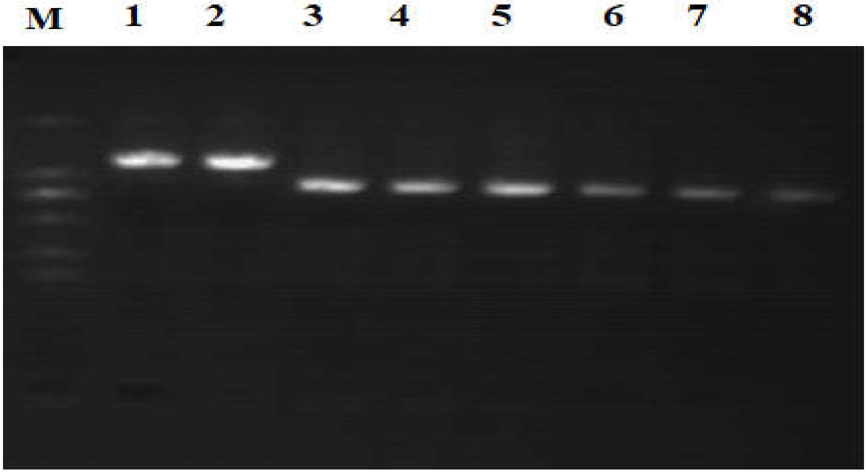

Fig. 1. The electrophoresis results from this study
From 1 to 8 are *rpl20-rps12*, *psbB-psbH*, *rpoC2-rps2* and *trnL–trnF*, respectively. M is the marker

The DNA sequences of *Arisaema* from NCBI were last downloaded on November 8, 2021. Duplicate and uncertain sequences were excluded. All obtained sequences were searched in BLAST (implemented by the National Center for Biotechnology Information (NCBI) http://www.ncbi.nlm.nih.gov) against the GenBank nucleotide database to test for contamination and to confirm the targeted markers. All correct sequences were aligned using MUSCLE v.3.8.31 (Edgar 2004), followed by manual adjustment in Geneious v.8.0.5 to make the final dataset matrix (Kearse *et al.*, 2012).

2.2. Phylogenetic analyses

The phylogenetic analyses of Vietnamese *Arisaema* were conducted using both maximum likelihood (ML) and Bayesian inference (BI) methods. The best-fitting model applied for the combined datasets by the Akaike Information Criterion (AIC) as implemented in jModelTest v.2.1.6 (Darriba *et al.*, 2012).

The ML analyses were performed using RAxML v.8.2.8 (Stamatakis 2014) available in the CIPRES Science Gateway (Miller *et al*., 2010), with the best-fitting substitution model and 1000 bootstrap replicates for statistical support. The Bayesian analysis was performed in MrBayes v.3.1.2 (Ronquist & Huelsenbeck 2003) on the CIPRES Science Gateway (Miller *et al.,* 2010) using the same best-fitting substitution model. The Markov chain Monte Carlo (MCMC) algorithm was run for 10 million generations with a total of four chains, starting from a random tree, and trees were sampled every 1000 generations. The program Tracer v.1.6 (Rambaut & Drummond, 2007) was used to check that effective sample sizes (ESSs) were attained for all relevant parameters assessed (>200). With the first 25% of sampled generations discarded as burn-in, the 50% majority-rule consensus tree and Bayesian posterior probabilities (PP) were obtained using the remaining trees.

3. RESULTS AND DISCUSSION

3.1. Phylogenetic relationships of Vietnamese Arisaema

We generated 8 sequences from the newly collected samples of Vietnamese *Arisaema*. The combined dataset resulted in a matrix of 2853 characters. The topology from ML and BI analyses of the combined dataset were highly congruent, only differing in low resolution nodes. We thus present the BI tree with BS and PP values in Fig.2.

Our phylogenetic analyses supported *Arisaema* as monophyletic, with 15 sections recognized within the genus (Fig. 2). This result is congruent with Ohi-Toma *et al.* (2016) and Tran *et al.* (2022). The polytomies are still distributed in the phylogenetic tree, however, placement and support values for most clades are improved.

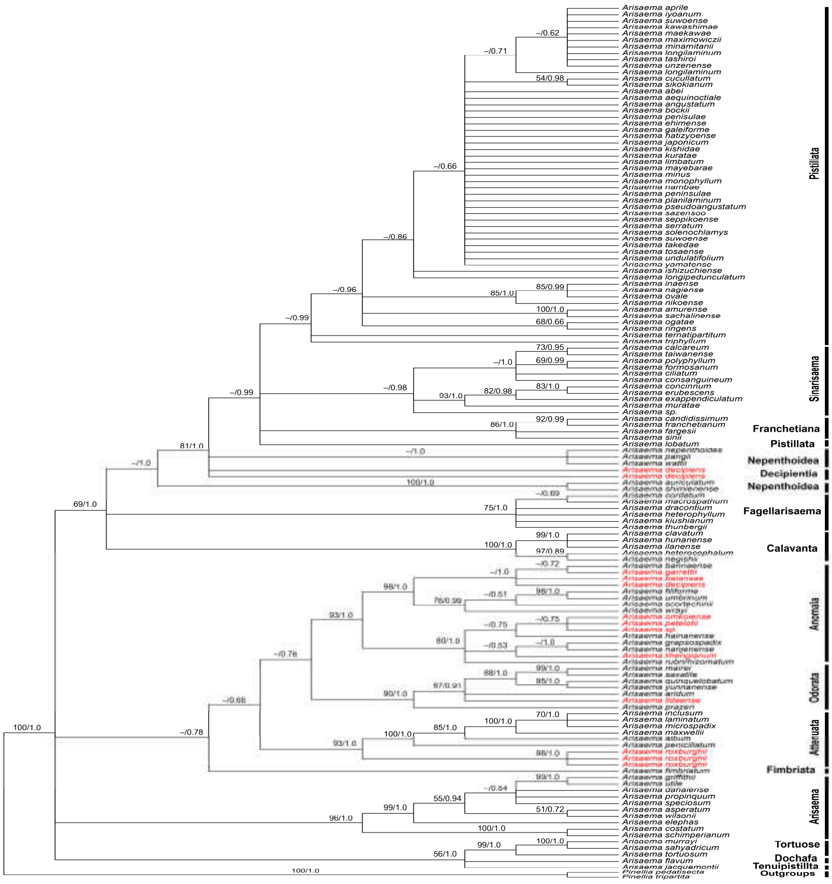

Fig. 2. Majority rule consensus tree of *Arisaema* based on the combined datasets of four DNA regions (*trnL–trnF*, *rpl20–rps12*, *psbB–psbH* and *rps2–rpoC2*). ML bootstrap values and posterior probabilities (PP) of the BI analysis are presented above the branches. "–" indicates the support values less than 50%. The circumscription of sections follows the classification of Ohi-Toma *et al.* (2016). *Arisaema* species in Vietnam are marked in red

Our results indicated that Vietnamese *Arisaema* is not monophyletic, the Vietnamese *Arisaema* species is nested in *Attenuata*, *Ordorata*, *Anomala* and *Decipientia* sections (Fig. 2). This result shows that the members of Vietnamese *Arisaema* are closely related and they placed within the Asian *Arisaema*. The three sections *Attenuata*, *Ordorata*, *Anomala* share the common ancestor (Fig. 2), they are endemic group in Asia with mophological characteristics such as: rhizomatous stem, trifoliolate leaf blade, appendix slender and covered by filiforme sterile flowers. It is likely that these species have adapted and evolved in tropical monsoon regions in southern China and Southeast Asia.

For *Arisaema decipiens*, the species with wide distribution in SW China, NE India, Myanmar, Vietnam, Ohi-Toma *et al.* (2016) suggested that this species was likely not monophyletic and the possition of this species is not stable, especially with individual from different areas such as Vietnam and China. This study confirmed that *A. decipiens* is non-monophyletic, the individual from Vietnam is separate from *Decipientia* section. We suggest that further study with a comprehensive sampling of this species is necessary to determine the phylogenetic position and genetic population of the species.

3.2. Origin and evolutionary history of Vietnamese Arisaema

Tran *et al.* (2022) suggested that *Arisaema* originated in Southeast Asia at 33.27 Ma during the early Oligocene, and soon after the initial origin *Arisaema* started to diverge at 31.28 Ma (Fig. 3). The results of divergence time estimations and ancestral area reconstruction analyses (Fig. 3) indicated that all Vietnamese *Arisaema* members originated in Southeast Asia since ca. 19 Ma during Mid-Miocene eventhough they do not share a common ancestor (Fig. 3), and subsequently diversified in Southeast Asia to make the current distribution.

Based on our observation in the field and suggestion from Mayo *et al.* (1998), *Arisaema* and several genera of Araceae prefer wet to swampy conditions, or grow near open water. They prefer growing in woodlands or in shady places under trees in deciduous forests and rainforests. *Arisaema* has few-seed berries with bright colors (orange, yellow, and red), and those fruits represent striking adaptations for birds and small rodents dispersal (Murata *et al.,* 1993; Wada & Uemura, 1994; Vogel & Martens, 2000; Renner *et al.,* 2004; Thomason 2020). Jetz *et al.* (2012) inferred that birds underwent a major increase in diversification rate since ca. 50 Ma. While, Fabre *et al.* (2012) suggested that many extant families of rodent originated during the Paleogene before the end of the Oligocene (ca. 31 Ma). Oliver *et al.* (2017) suggested that Ctenodactylidae (Rodentia) from Mongolia has an initial burst in diversification in the early Oligocene. Therefore, it is likely that the dispersal and diversification of *Arisaema* were closely related to birds and rodents.

Forests (including tropical forests and temperate forests or mountainous forests at high elevation) were present throughout the Northern Hemisphere during the early Cenozoic, which allowed for intercontinental dispersal of plants (Wei *et al*., 2015; West *et al*., 2015). *Arisaema* can be harbored in both tropical forests and temperate forests, and many *Arisaema* species have occurred in the deciduous forests and subalpine forests in East Asia and East North America (Murata 1984, 1990; Mayo *et al*., 1997; Gusman & Gusman 2002; Govaerts *et al*., 2002; Murata *et al*., 2013; Ohi-Toma *et al*., 2016).

The global climate was warm since the late Oligocene and early Miocene before it became optimum (warm and wet) in Mid-Miocene (Zachos *et al*., 2001). The forests were present during Mid-Miocene in Southeast Asian. Thus, we hypothesize that after originating in Southeast Asia during the Oligocene, *Arisaema* diverged in this area and then migrated to Vietnam during climate optimum period of Mid-Miocene.

Our results also indicate that, Vietnamese *Arisaema* do not have any connection with *Arisaema* from India and North China, Japan and the Korean Peninsula regions (Fig. 3).

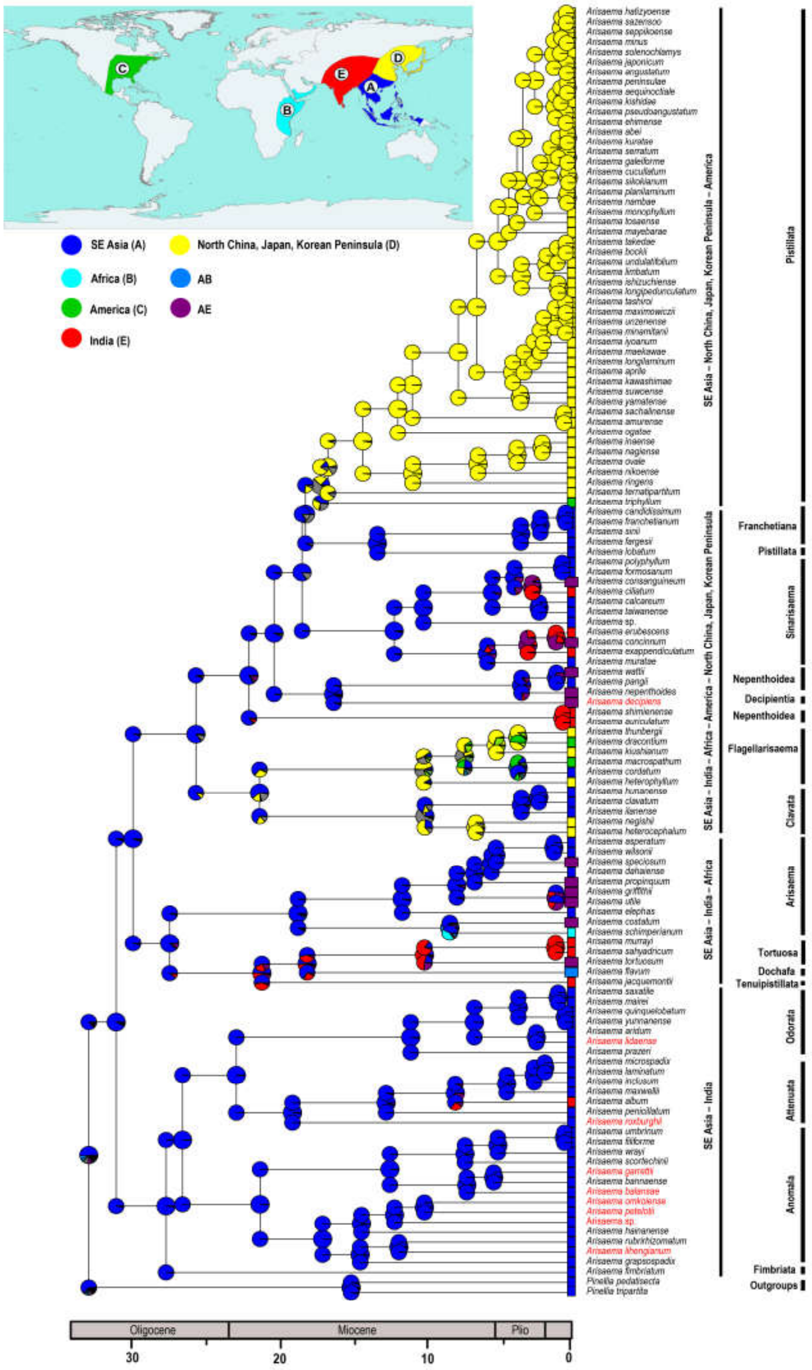

Fig. 3. Ancestral area reconstruction of *Arisaema* by BioGeoBEARS (*j* = 0.000517, LnL = −115.90) Geologic time scale is shown at the bottom. Area abbreviations are as follows: A: Southeast (SE) Asia (including mainland of Southeast Asia, Indochina and Malesia, but excluding New Guinea); B: Africa (including the coastal area of the Arabian Peninsula and East Africa); C: America (including North America, Mexico); D: North China, Japan, the Korean Peninsula region (NJK region); E: Himalayas (including E Pakistan, N India, Himalaya region, and SW China).
***Arisaema* species in Vietnam marked in red**

4. CONCLUSION

This study represents a comprehensive phylogenetic and biogeographic reconstruction of the genus *Arisaema* by exploring the molecular phylogeny and evolutionary history of Vietnamese *Arisaema*. The genus *Arisaema* originated in Southeast Asia at ca. 31 Ma during the Oligocene, and members of Vietnamese *Arisaema* derived from the Southeast Asia *Arisaema* during climate optimum period of Mid-Miocene with the presence and development of the tropical rainforest.

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LỊCH SỬ PHÁT SINH LOÀI VÀ TIẾN HÓA CỦA CHI NAM TINH VIỆT NAM (HỌ RÁY)

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TÓM TẮT

Trong họ Araceae, chi Arisaema là một trong những chi lớn nhất với 200 loài trên thế giới và phân bố chủ yếu ở các khu vực ôn đới và ôn đới ấm từ Đông đến Đông Nam của Bắc Mỹ đến Bắc Mexico, từ nhiệt đới Đông và Đông Bắc Phi đến Ả Rập và từ vùng ôn đới Đông Á đến Nam và Đông Nam Á. Một số loài Arisaema được sử dụng làm thực phẩm và thuốc địa phương ở Ấn Độ, Trung Quốc và Việt Nam. Việc khám phá mối quan hệ giữa các loài thực vật và giải thích nguồn gốc thực vật và cách chúng di cư giữa các khu vực trên thế giới và ở Việt Nam vẫn còn là một thách thức. Việc xây dựng phát sinh loài phân tử, ước tính thời gian phân hóa và diện tích tổ tiên của các dòng họ dựa trên bằng chứng về dữ liệu phân tử, hóa thạch, địa chất đã cung cấp những hiểu biết chính về sự tiến hóa của thực vật. Nghiên cứu này được thực hiện dựa trên việc lấy mẫu đơn vị phân loại toàn diện và dữ liệu phân tử DNA lục lạp từ bốn vùng của chi Nam Tinh để xác định lịch sử phát sinh loài và tiến hóa của chi Nam Tinh Việt Nam (Họ Ráy). Sự phát sinh loài của chi Nam Tinh được nghiên cứu bằng cách sử dụng các phương pháp ML và BI. Kết quả của chúng tôi chỉ ra rằng chi Nam Tinh có nguồn gốc từ Đông Nam Á vào khoảng 31 triệu năm trong thời kỳ Oligocen và chi Nam Tinh Việt Nam có nguồn gốc từ chi Nam Tinh Đông Nam Á trong thời kỳ khí hậu tối ưu giữa thời kỳ Miocen với sự hiện diện và phát triển của rừng mưa nhiệt đới. Trong khi đó, chi Nam Tinh Việt Nam dường như không có bất kỳ mối liên hệ nào với chi Nam Tinh đến từ Ấn Độ, Bắc Trung Quốc, Nhật Bản và các khu vực bán đảo Triều Tiên.

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