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Molecular systematics and historical biogeography of Araceae at a worldwide scale and in Southeast Asia

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Contents

Preface

Statutory Declaration

Erklärung

Diese Dissertation wurde im Sinne von §12 der Promotionsordnung von Prof. Susanne S. Renner betreut. Ich erkläre hiermit, dass die Dissertation nicht einer anderen Prüfungskommission vorgelegt worden ist und dass ich mich nicht anderweitig einer Doktorprüfung ohne Erfolg unterzogen habe.

Ehrenwörtliche Versicherung

Ich versichere hiermit ehrenwörtlich, dass die vorgelegte Dissertation von mir selbständig und ohne unerlaubte Hilfe angefertigt wurde.

Lars Nauheimer

1. Gutachter: Prof. Susanne S. Renner
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List of Publications

In this thesis, I present the results from my doctoral research, carried out in Munich from April 2009 to April 2012 under the supervision of Prof. Susanne S. Renner. My results have contributed to two manuscripts presented in Chapters 2 and 3, and published in peer-reviewed journals. Oral and poster presentations are also listed below.

Peer-reviewed journal articles

- **Nauheimer L**, Boyce PC, and Renner SS. 2012. Giant taro and its relatives: A phylogeny of the large genus *Alocasia* (Araceae) sheds light on Miocene floristic exchange in the Malesian region. *Molecular Phylogenetics and Evolution* 63: 43–51.
- **Nauheimer L**, Metzler D, and Renner SS. 2012. Global history of the ancient monocot family Araceae inferred with models accounting for past continental positions and previous ranges based on fossils. *New Phytologist* 195: 938–950.

Declaration of contribution as co-author

The two publications, presented in Chapter 2 and Chapter 3 of this thesis, result from collaboration with my supervisor Prof. Susanne S. Renner (SR), Dr. Peter C. Boyce (PB), and Prof. Dirk Metzler (DM).

I carried out all data collection, fieldwork, and all analyses; Prof. Metzler helped with the molecular clock dating runs in TreeTime (Chapter 2). Interpretation of results and writing of the manuscript were carried out in close collaboration with SR, and plant determinations for Chapter 3 were provided or confirmed by PB.

Note

In the course of my dissertation, I was able to visit eight international conferences in Zurich, Nancy, Bavaria, Bali, Singapore, Berlin, and Melbourne, conduct fieldwork in Sarawak and Sabah, and carry out herbarium work in the 13 herbaria listed below. My herbarium work focused on the morphology and distribution of *Alocasia* species and served to collect leaf samples for DNA isolation. More than 2800 vouchers were investigated and documented photographically. The fieldwork provided insight into the ecology and habitats of *Alocasia* and its close relatives; it also yielded 97 herbarium collections and silica-dried leaf samples.

Conferences attended

- Niche Evolution, Zurich, Switzerland, July 2009 (attendance)
- 10th Aroid Conference, Nancy, France, July 2009 (poster presentation)
- VW-Statussymposium, Frauenchiemsee, Germany, May 2010 (poster presentation)
- International Meeting of the Association for Tropical Biology and Conservation (ATBC), Bali, Indonesia, July 2010 (oral presentation)
- 8th Flora Malesiana Symposium, Singapore, August 2010 (oral presentation)
- Ecology, Evolution, and Systematics Conference, Munich, Germany, October 2010 (organization)
- Biosystematics, Berlin, Germany, February 2011 (oral presentation)
- 18th International Botanical Congress (IBC), Melbourne, Australia, July 2011 (oral presentation)

Oral presentations

- **Nauheimer L**, Boyce PC, Renner SS. Biogeography of *Alocasia* (Araceae): Colonization of the Malay Archipelago. *2010 ATBC conference, July 2010, Bali, Indonesia.*
- **Nauheimer L**, Boyce PC, Bogner J, Renner SS. The evolution and biogeography of *Alocasia*, *Colocasia*, and related genera. *8th Flora Malesiana Symposium, August 2010, Singapore.*
- **Nauheimer L**, Boyce PC, Renner SS. Reconstructing the biogeography of the 100 species of a Miocene Asian/Australian clade. *Biosystematics, February 2011, Berlin, Germany.*
- **Nauheimer L**, Cusimano N, Chartier M, Bogner J, Renner SS. The family Araceae in space and time. *18th IBC, July, 2011, Melbourne, Australia.*

Poster presentations

- **Nauheimer L**, Boyce PC, Renner SS. Phylogeny and biogeography of *Alocasia* (Araceae), and a DNA-based identification service. *10th Aroid Conference*, July 2009, Nancy, France. Small version on page 104.
- **Nauheimer L**, Boyce PC, Renner SS. Biogeography of *Alocasia* (Araceae): Colonization of the Malay Archipelago. *2nd Status Symposium in Evolutionary Biology*, May 2010, Fraueninsel, Germany. Small version on page 106.

Herbaria visited

- Herbarium München (M), Germany, 2009–2012
- Herbarium Zürich (Z), Switzerland, July 2009
- Herbarium Berlin (B), Germany, November 2009
- Herbarium Leiden (L), March 2010
- Herbarium Botanic Garden Bali, Indonesia, July 2010

- Herbarium Bogor (BO), Indonesia, July 2010
- Herbarium Kuching (SAR), Malaysia, August 2010
- Herbarium Singapore Botanic Gardens (SING), Singapore, August 2010
- Herbarium Kinabalu Parks (SNP), Malaysia, August 2010
- Herbarium Sandakan (SAN), Malaysia, September 2010
- Herbarium University Kuala Lumpur (KLU), Malaysia, September 2010
- Herbarium Forest Research Institute Malaysia (FRI), Malaysia, September 2010
- Herbarium Sydney (NSW), Australia, August 2011

Fieldwork

- Malaysia, Sarawak, August 2010
- Malaysia, Sabah, August/September 2010

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- Elite Network of Bavaria; salary for two years
- German Research Foundation (DFG, RE 603/11-1); laboratory and travel expenses
- Gesellschaft der Freunde des Botanischen Gartens München e.V.; travel expenses to Nancy, France and Leiden, Netherlands

Summary

This dissertation addresses the biogeographic history of the Araceae family and of one of its largest genera, *Alocasia*. With >3300 species, Araceae are among the largest families of flowering plants. It is the monocot lineage with the deepest fossil record, reaching back to the Early Cretaceous. Araceae are distributed worldwide, but >3100 species occur in the tropical regions of the Americas, Asia, Africa, and Australia; most fossils from the Late Cretaceous and many younger ones come from the temperate zone in the northern hemisphere, implying much extinction and range expansion. Most subfamilies are pantropically distributed, and almost all genera are restricted to one continent.

Alocasia comprises 113 species, many as yet undescribed, making it the 7th-largest genus of the Araceae. Many species are ornamentals, and two species are of interest for man, either for food (giant taro) or in local cultures (Chinese taro). The origin of these species was not known. *Alocasia* is distributed in Southeast Asia from India to Australia, with species occurring on all islands of the Malay Archipelago. This region has a complex geologic history shaped by the collision of the Eurasian, the Pacific, and the Indo-Australian plate. The Malesian flora and fauna comprises Laurasian and Gondwanan elements, reflecting the influence of changing sea levels, uplift and submergence of islands, and other tectonic movement.

In this thesis, I used molecular phylogenetics, Bayesian divergence dating, ancestral area reconstruction to understand the past distribution of the Araceae family and the *Alocasia* clade in the context of past continent movements and climate history.

For the family analysis, existing chloroplast DNA matrices were augmented so that all Araceae genera were represented by one or more species, with a focus on covering geographic disjunctions, especially between continents. Divergence dating relied on seven confidently assigned fossil constraints, comparing uniform and gamma-shaped prior distributions on fossil ages, as well as several molecular clock models. Biogeographic analyses were performed in a model-based likelihood framework that took into account past dispersal routes based on continent connectivity and climate. I also integrated fossils into the ancestral area reconstruction, either simulating extinct or still existing ranges, and then compared results to those obtained from analyses without fossils.

To study the morphology and ecology of *Alocasia*, fieldwork was conducted in Malaysia and herbarium work in Germany, the Netherlands, Indonesia, Malaysia, and Singapore. Maximum likelihood phylogenies were inferred based on chloroplast and nuclear loci, sequenced for 71 species of *Alocasia* plus 25 outgroup species from 16 genera. Bayesian divergence dating of the nuclear phylogeny relied on one fossil constraint and ancestral areas were reconstructed using parsimony- and likelihood-based methods.

The Araceae diverged from the remaining Alismatales in the Early Cretaceous (ca. 135 Ma ago), and all eight subfamilies originated before the Cenozoic. The earliest lineages are inferred to have occurred in Laurasia (based on fossils and tree topology), and most lineages reached Africa, South America, Southeast Asia, and Australia during the Paleogene and Neogene. Many clades experienced extinction in the temperate regions of the northern hemisphere during the Oligocene climate cooling. Two continentally disjunct genera (*Nephthytis* and *Philodendron*) are polyphyletic and need taxonomic rearrangement. Plastid substitution rates are exceptionally high in free-floating and water-associated Araceae. Ancestral area reconstructions obtained when fossil (no longer occupied) ranges where included in the analyses were more plausible than those without fossil ranges. This is not a trivial result because only in a quantitative (computer-based) analysis is it possible for fossil ranges to influence results (here areas) at distant nodes in the phylogenetic tree.

The nuclear and plastid phylogenies of *Alocasia* revealed the polyphyly of the two genera *Alocasia* and *Colocasia*; to achieve monophyly, two species (*Alocasia hypnosa* and *Colocasia gigantea*) have to be moved to other genera. There were strong incongruencies

between phylogenies from the two partitions: The chloroplast data reflect geographical proximity, the nuclear morphological similarity. This may indicate hybridization events followed by chloroplast capture. Based on the nuclear tree, *Alocasia* split from its sister group by the end of the Oligocene (ca. 24 Ma) and colonized the Malay Archipelago from the Asian mainland. Borneo played a central role, with 11–13 of 18–19 inferred dispersal events originating there. The Philippines were reached from Borneo 4–5 times in the late Miocene and early Pliocene, and the Asian mainland 6–7 times during the Pliocene. The geographic origin of two domesticated species could be resolved: Giant taro originated on the Philippines and Chinese taro on the Asian mainland.

Zusammenfassung

Diese Doktorarbeit behandelt die historische Biogeografie der Araceen und eine ihrer artenreichsten Gattungen, *Alocasia*. Die Araceen sind mit über 3300 Arten unter den größten Familien der Blütenpflanzen. Sie sind weltweit verbreitet, wobei der Großteil (>3100 Arten) in den tropischen Regionen von Amerika, Asien, Afrika und Australien vorkommt. Die ältesten Fossilien der Monokotyledonen überhaupt sind Araceenfossilien aus der Unterkreide. Diese und viele der jüngeren Fossilien stammen jedoch aus gemäßigten Gebieten der nördlichen Hemisphäre, was auf ausgestorbene Abstammungslinien und Veränderungen der Verbreitungsgebiete hindeutet.

Mit 113 Arten ist *Alocasia* die 7. größte Gattung der Araceen. Viele Arten sind Zierpflanzen, wobei zwei Arten als Nahrung (Riesen-Taro) oder aus kulturellen Gründen (chinesischer Taro) abgebaut werden, deren geografischer Ursprung jedoch nicht bekannt ist. Die Gattung *Alocasia* ist von Indien über ganz Südostasien bis nach Australien verbreitet und kommt auf jeder größeren Insel im Malaiischen Archipel vor. Diese Region hat eine komplexe geologische Geschichte, die von den Kollisionen der Pazifischen, Indisch-Australischen und Eurasischen Kontinentalplatten bestimmt wurde. Die Flora und Fauna in dem Malaiischen Archipel besteht aus laurasichen und gondwanischen Elementen, deren jeweilige Verbreitung durch schwankende Meeresspiegel, dem Auf- und Abtauchen von Inseln und anderen tektonischen Prozessen beeinflusst wurde.

In dieser Dissertation rekonstruierte ich ehemalige Verbreitungsgebiete und Ausbreitungswege mit Hilfe von molekularer Phylogenetik und Bayes'scher Altersbestimmung, um die frühere Verbreitung der Araceen sowie von *Alocasia* im Kontext der Kontinentalbewegungen und der Klimageschichte zu verstehen.

Für die Familiendatierung wurde eine Matrix von Chloroplasten Sequenzen derart erweitert, dass alle Gattungen mit mindestens einer Art vertreten sind und sofern eine Gattung geographisch disjunkt vorkommt (insbesondere zwischen Kontinenten) diese von einer mindestens Art pro Region vertreten ist. Die Altersbestimmung beruhte auf der Kalibrierung mit sieben Fossilien, dem Vergleich zwischen uniform- und gammaförmigen Priorverteilungen, sowie der Gegenüberstellung mehrerer Modelle molekularer Uhren. Biogeografische Analysen wurden mit Hilfe von einer Modell basierten Wahrscheinlichkeits-(likelihood") Methode durchgeführt, die frühere Ausbreitungswege aufgrund vergangener Kontinentalbewegungen und Klimaänderungen in Betracht ziehen kann. Zusätzlich habe ich Fossilien in die Rekonstruktion ehemaliger Verbreitungsgebiete eingebunden, entweder ausgestorbene oder noch lebende Arten simulierend, und die Ergebnisse mit den Analysen ohne Fossilien verglichen.

Um die Morphologie und Ökologie von *Alocasia* zu untersuchen, habe ich Feldarbeit in Malaysia und Herbariumsarbeit in Deutschland, den Niederlanden, Indonesien, Malaysia und Singapur durchgeführt. Phylogenien, basierend auf Chloroplasten- und Kern-Sequenzen, wurden für 71 *Alocasia* Arten und 25 Außengruppenarten aus 16 Gattungen erstellt. Bayes'sche Altersbestimmung der nukleären Phylogenie wurde mit einem Fossil kalibriert und die Rekonstruktion ehemaliger Verbreitungsgebiete wurde mit Sparsamkeits- („parsimony") und Wahrscheinlichkeits- („likelihood") Methoden durchgeführt.

Die Araceen haben sich zu Beginn der Unterkreide (vor ca. 135 Ma) von den übrigen Alismatales abgespalten. Alle acht Unterfamilien existierten schon vor dem Paläogen. Die Rekonstruktionen zeigen, dass die ersten Araceen in Laurasien verbreitet waren (basierend auf Fossilfunden und Stammbaumtopologie), und die meisten Abstammungslinien erreichten Afrika, Südamerika, Südostasien und Australien im Paläogen und Neogen. Viele Stammlinien sind während der Abkühlung des Klimas im Oligozän in den gemäßigten Regionen der nördlichen Hemisphäre ausgestorben. Zwei disjunkt verbreitete Gattungen (*Nephthytis* und *Philodendron*) sind polyphyletisch und benötigen taxonomische Bearbeitung. Plastidäre Substitutionsraten sind außergewöhnlich hoch in den freischwimmenden und wasserassoziierten Araceen sowie in basalen Abstammungslinien. Die Rekonstruktion ehemaliger Verbreitungsgebiete ist glaubwürdiger, wenn Fossilen in die Analysen eingebunden wurden. Dies ist kein triviales Ergebnis, denn nur in einer quantitativen Analyse ist es möglich, dass Fossilien die Rekonstruktionen entfernter Knoten in einer Phylogenie beeinflussen.

Die Phylogenien von *Alocasia* enthüllten, dass *Alocasia* und *Colocasia* polyphyletisch sind. Um deren Monophylie wieder herzustellen, müssen zwei Arten (*Alocasia hypnosa* und *Colocasia gigantea*) in andere Gattungen verlegt werden. Es ergaben sich gut gestützte topologische Unterschiede zwischen den nukleären und plastidären Phylogenien. In der plastidären Phylogenie sind Arten nach ihrer geografischen Verbreitung gruppiert, in der nukleären Phylogenie nach morphologischer Ähnlichkeit. Dies deutet auf Hybridisierung mit anschließendem 'chloroplast capture' hin. Basierend auf dem nukleären Stammbaum hat sich *Alocasia* zum Ende des Oligozäns hin (vor ca. 24 Ma) von der Schwestergruppe abgespalten und den Malaiischen Archipel vom asiatischen Festland aus besiedelt. Borneo, von wo 11–13 der 18–19 Ausbreitungen ausgingen, spielte dabei eine zentrale Rolle. Die Philippinen wurden von Borneo aus 4–5-mal im späten Miozän und frühen Paläogen besiedelt, und das asiatische Festland 6–7-mal im Pliozän. Die geografische Herkunft der zwei domestizierten Arten konnte geklärt werden: Riesen-Taro kommt von den Philippinen und Chinesischer Taro vom asiatischen Festland.

1

Introduction

General Introduction

Understanding the historical processes and present-day ecological conditions that determine species distribution is the focus of biogeographic research. Molecular phylogenies combined with ancestral area reconstructions allow inferring the geographic direction of clade expansion, and molecular clock dating allows correlating past geologic, climatic, or biologic events to divergence events in a molecular tree. In combination, these methods have led to a new flowering of biogeography during the past 20 years (Renner, 2005; Crisp et al., 2011).

In this thesis, I use phylogenetics, molecular clock dating, and ancestral area reconstruction to investigate the biogeographic histories of two plant clades. My focal group is the species-rich and horticulturally important Araceae, a family of worldwide distribution and with a rich fossil record. In one study, I use a fossil-calibrated phylogeny of the entire family to shed light on the origin and early diversification of Araceae, a history reaching back to the Early Cretaceous. In a second study, I focus on the large Araceae genus *Alocasia*, with more than 100 species, to understand its distribution across Southeast Asia, including the Malay Archipelago.

Estimating Divergence Times

Estimation of divergence times based on molecular sequences has become an indispensable part of evolutionary studies dealing with historical processes (Renner, 2005, for a review). The approach is based on molecular clock hypothesis (Zuckerkandl and Pauling, 1965), which takes as its premise that in large enough samples, mutations and substitutions accumulate sufficiently regularly to provide a rough measure of time, comparable to the ticking of a clock, hence the name molecular clock. Knowledge of the divergence times of two lineages in a molecular tree can be used to calibrate substitution accumulation, and the resulting rate (substitutions $\cdot$ site$^{-1}\cdot$ time^{-1}) can then be used to calculate the divergence times (ages) of related lineages. The molecular clock hypothesis is now almost 50 years old and has been abundantly tested. In biogeography, it has led to a flowering of "deep time" investigations, focusing on relatively old clades of wide, often disjunct distributions. These analyses have benefited from the increasing availability of molecular sequence data combined with constantly improving software and computing power. It is well understood, however, that there is no universal molecular clock and that substitution rates vary among lineages, nuclear, plastid, and mitochondrial genome, DNA loci, and within clades across time (a phenomenon called heterotachy; Lopez et al., 2002).

Reasons for different substitution rates in organisms are manifold and have been related to body size, population dynamics, or life history (Smith and Donoghue, 2008; Bromham, 2009), but there is no well-understood mechanism explaining these putative correlations (Lynch, 2007). Attempts to address rate variation among lineages are the so-called "relaxed-clock" models, which assume rate changes across the phylogeny. Most important among relaxed clock approaches are non-parametric rate smoothing (Sanderson, 1997), penalized likelihood in "r8s" (Sanderson, 2002), and Bayesian relaxed-clock methods implemented in "Multidivtime" (Thorne and Kishino, 2002), "Bayesian Evolutionary Analysis Sampling Trees" or "BEAST" (Drummond et al., 2006, 2012), and "TreeTime" (Himmelmann and Metzler, 2009). Results obtained with relaxed clock models should be compared to strict clock models (for the same dataset) since inference of divergence times from DNA is based on the premise of more or less clock-like data.

Fossil calibration Of crucial importance for inferring divergence dates is the calibration of the molecular clock. In historical biogeography, this is achieved using fossils assigned to nodes in a phylogeny or, more rarely, by geological constraints such as the emergence of islands or continent connectivity. The age of a fossil can provide a minimum age for the clade to which it belongs based on some morphological synapomorphy seen in the fossil and only found in the species group derived from the node to which the fossil is assigned. In other words, a fossil calibration should be applied as a minimum constraint for the stem lineage of the clade to which the fossil belongs (Doyle and Donoghue, 1993; Renner, 2005; Benton and Donoghue, 2007). For finding the proper placement of a fossil, molecular phylogeneticists depend on the work of palaeobotanists, and for finding the proper age of a fossil, they depend on geological information concerning the horizons and formations in which a particular fossil was found. In my own work, I have encountered several difficult and controversial fossil determinations (e.g., Friis et al., 2004; Heimhofer et al., 2007; Hofmann and Zetter, 2010; details in Chapter 2), which emphases the importance of critical fossil assignments (Chapter 2, Supplementary Table 2).

In the absence of fossil data or to cross-validate fossil-based divergence times, one can use average substitution rates from other studies or from meta-analyses (Kay et al., 2006), and this type of cross validation has been applied in numerous studies (e.g., Wolfe et al., 1989; Chacón et al., 2012; Filipowicz and Renner, 2012). Alternatively, one can compare results obtained by using ingroup fossils with results from using "secondary" calibration, defined as the application of a node age inferred in another molecular clock study with overlapping taxon sampling (examples of studies from the lab in which I carried out my research that have used this approach are Schaefer et al., 2009; Michalak et al., 2010). Particularly useful for finding potential secondary calibration points are studies of the entire angiosperms or all monocots, such as Bremer (2000), Wikström et al. (2001), Janssen and Bremer (2004), Bell et al. (2005, 2010), and Smith et al. (2010).

Historical Biogeography

Historical biogeography focuses on higher taxonomic groups and on large time scales, often covering millions of years. It is not to be confused with phylogeography, which investigates processes at the population level and usually over short(er) time periods (Avise, 2009). Biogeography is an integrative research field that combines data from biology, ecology, climatology, geology, and palaeobiology. Following the general acceptance of plate tectonics in the 1960s, biogeography swung from dispersal as the default explanation for disjunct distributions to moving plates as the default explanation (Nelson and Platnick, 1981). With molecular clock dating, the pendulum has now swung back to dispersal as the default explanation (at least in most flowering plant clades), with ancient overland dispersal as the rare exception. Today, the paradigm is that if a geographic disjunction between sister taxa is younger than the respective plate movement or other overland connection, it is inferred as due to long-distance dispersal. Obviously, such inferences remain weak because of the huge error ranges in both the dating of tectonic movements (or other types of land bridges) and the dating of clade divergence times. Another problem is that this type of inference is essentially restricted to trans-oceanic disjunctions (or disjunctions involving other inhospitable intervening areas, such as ice caps or mountain ranges) and cannot address long-distance dispersal over hospitable land.

Ancestral area reconstruction The main approach used to infer past ranges or range shifts is the so-called ancestral area reconstruction. Methods have become increasingly sophisticated (Lamm and Redelings, 2009). Parsimony, as used for ancestral state reconstructions (e.g., implemented in Mesquite; Maddison and Maddison, 2011), finds the ancestral states, by reducing the number of character changes (in this case areas), but does not take into account extinction or dispersal. Dispersal-vicariance-analysis (DIVA; Ronquist, 1997) was the first approach to integrate dispersal, extinction, and area vicariance by allowing a minimum number of dispersal or extinction events on a cladogram and permitting the combined occurrence of taxa in a region. The dispersal-extinction-cladogenesis model (DEC, implanted in the software "Lagrange"; Ree et al., 2005; Ree and Smith, 2008) took this approach further by estimating probabilities of geographic ranges along nodes and branches, given genetic branch lengths and user-defined dispersal probabilities between areas and across time. Bayesian methods have also been applied in biogeographic analyses and are the only approach that simultaneously carries out tree searching and ancestral area reconstruction. They do not allow combined areas and are thus useful only for highly motile organism, such as pathogens or viruses, where vicariance plays essentially no role (Lemey et al., 2009; Pirie et al., 2012). Another approach is Bayes-DIVA (Nylander et al., 2008), implemented in "S-DIVA" (Yu et al., 2010), which applies the DIVA approach to numerous trees from MCMC chains, thus attempting to account for topological uncertainty. Calculation times required for parameter-rich DEC runs far exceed those required for parsimony reconstructions using DIVA, and application to multiple trees is feasible only for small datasets, e.g., the *Caprifolium* clade of *Lonicera* (Caprifoliaceae; Smith and Donoghue, 2010) and *Linaria* sect. *Versicolores* (Fernández-Mazuecos and Vargas, 2011).

Today, DIVA remains the most widely used method, while the much more computationally intensive DEC approach has been used in relatively few studies. I have used both methods in my work (Chapters 2 and 3). As explained above, DIVA minimizes dispersal and extinction but permits large (combined) ancestral areas, assumed to have fragmented over time. The user can cap the maximal number of combined areas, but this involves *a priori* assumptions that can be difficult to support by specific biological or geological arguments. It is usually biologically implausible that ancestors had huge (even worldwide) ranges that became ever more fragmented (i.e., vicariant).

The "large-ancestral area problem" persists in the DEC approach (Ree et al., 2005; Ree and Smith, 2008), although for a different reason than in DIVA; it occurs when estimated extinction rates are low, for example, when long-branched basal lineages have survived and are sampled (Ree et al., 2005).

A major advance of the DEC approach is that the user can adjust the dispersal probabilities between areas and across time. This permits to incorporate *a priori* knowledge of past dispersal routes, which may be available based on knowledge of an area's geologic or climatic history. Therefore, DEC is especially suitable for reconstructing ancestral ranges of ancient clades with worldwide distribution that may have been affected by the break-up of Gondwana and climatic changes since the Cretaceous. It has been used to infer biogeographic histories of the Sapindaceae (Buerki et al., 2011) and the Simaroubaceae (Clayton et al., 2009), both reaching back to the Cretaceous, and for the even older Cupressaceae (Mao et al., 2012). Dispersal matrices can also be used to compare competing theories of past dispersal routes, as done for the Annonaceae (Couvreur et al., 2011), where a boreotropical migration was preferred over dispersal across the rafting Indian continent.

Incorporation of fossil ranges Fossils provide two kinds of information, the earliest age of a clade and the presence of a clade in some area at a particular time. Until recently, biogeographers focusing on molecular clocks and ancestral area reconstructions only used information about "minimum" ages. They did not use information about the presence of a clade in a particular area because fossil (extinct) ranges have not been incorporated into analyses directly. This was a disadvantage because ranges of extinct taxa provide information about the former range extension of a clade that is just as important, or more important, for ancestral area reconstruction than is a clade's minimal age. Many pantropically-distributed families have fossil records (usually from the Eocene or older epochs) in areas where they no longer occur; examples come from the Melastomataceae (Renner et al., 2001), Meliaceae (Muellner et al., 2006), Simaroubaceae (Clayton et al., 2009), Cupressaceae (Mao et al., 2012), and also the Araceae, the focus of my research, (Smith and Stockey, 2003; Wilde et al., 2005; Hofmann and Zetter, 2010). Before my work, only Clayton et al. (2009) and (Mao et al., 2012, simultaneous with my work) included fossil ranges directly into their ancestral area reconstructions. They did this by adding fossil taxa (similar to extant species) into a newick-format phylogenetic tree, with the branch length according to the fossil age and as sister to the clade the respective fossil had been assigned to.

The combination of model-based biogeographic methods that take into account past dispersal routes based on continent movement and climate changes with fossil distributions allows a more realistic reconstruction of the biogeographic history of lineages than ever before. Clayton et al. (2009) found that long-distance dispersal largely shaped the distribution of the Simaroubaceae family and Mao et al. (2012) could show that the break-up of Pangea resulted in the divergence of the two major lineages found in today's Cupressaceae.

The Araceae family was especially promising for such a study because of its nearly world-wide distribution, deep fossil record, and already relatively well understood phylogeny. It is a species-rich ancestral monocot lineage with striking geographic disjunctions (some examples are given below), yet most species show no obvious adaptations for long-distance dispersal. Its fossil record allows both multi-fossil calibrated molecular clock models and integration of fossil ranges into biogeographic analyses.

The Araceae Family

General introduction The Araceae family comprises >3300 described and >5400 estimated species (Croat and Boyce, 2012; 10^{th} January, 2012), and may be the 13^{th} largest family of flowering plants (`http://www.mobot.org/mobot/research/apweb/`). Many of its species are of horticultural interest. Araceae are herbs, often adapted to wet habitats, but also occur in arid areas and as epiphytes in the rainforest canopies. The foliage is variable with a complex venation pattern. This particularity, which is uncommon in monocotyledons, facilitates identification of genera and assignment of leaf fossils. Characteristic for the family is the inflorescence. It consists of an un-branched spike (spadix) with tightly packed and spirally arranged flowers, which is sheathed by a bract (spathe). The numerous flowers are generally small and extremely reduced. Two types of flower arrangement exists in the Araceae, bisexual flowers exposed on the spadix and uni-sexual flowers often at least partly covered by the spathe, and which might be highly specialized and often used to trap pollinators. Some species show thermogenesis in the sterile appendix of the spadix (e.g., *Colocasia esculenta*, *C. gigantea*, or *Alocasia macrorrhizos*; Ivancic et al., 2004, 2005, 2007). The spathe often protects the developing inflorescence or fruits and usually plays an important role for pollination; it attracts pollinators visually, traps them, or protects them to secure pollination (Gibernau et al., 2010). Pollinators and floral visitors belong mainly to three groups (Gibernau, 2003), bees (for instance in *Anthurium*, *Spathiphyllum*), beetles (in *Urospatha*, *Philodendron*), and flies (in *Alocasia*, *Amorphophallus*, *Arum*). Fruits are mostly juicy berries of reddish or orange color and usually dispersed by birds or mammals (Mayo et al., 1997). Many Araceae contain calcium oxalate crystals (raphides) and irritating latex for protection against herbivores (Mayo et al., 1997). Araceae chromosomes show high variation in number, size, and morphology. Counts are available for 26 % of all species and range from $2n = 8$ in *Typhonium* to $2n = 168$ in *Cryptocoryne* with an estimated ancestral haploid number of $n = 16$ (Cusimano et al., 2012).

Taxonomy The Araceae family belongs to the order Alismatales. It is the sister group to a clade formed by the 13 other families in this group and represents one of the earliest-diverging lineages in the monocots. The first monographer of the family was Heinrich Wilhelm Schott (1794–1865). He described ca. 900 species and provided the first solid classification of the Araceae. The next person to focus on the Araceae was Adolf Engler (1844–1930) who worked from 1871 to 1878 as scientific assistant at the "Botanische Staatssammlung" in Munich. The most recent botanist in Munich to have worked on Araceae is Josef Bogner (Bogner, 1978; Bogner and Nicolson, 1991; Mayo et al., 1997). Bogner's long-standing interest in the family has resulted in significant aroid collections in the Munich Botanical Garden and Munich herbaria (M and MSB), and these have greatly contributed to this thesis.

Molecular phylogenetic methods were first brought to bear on the Araceae by French et al. (1995). These workers constructed a phylogeny based on chloroplast restriction site data for species representing most genera then recognized (86) and confirmed Engler's suspicion that Lemnaceae are part of the Araceae and are not close to *Pistia*. They also confirmed Grayum's (1987) conclusion based on morphology that *Acorus* is not an Araceae. The phylogeny of Cabrera et al. (2008), based on four plastid regions (>5000 basepairs) for 102 genera (one accession per genus), confirmed many findings of French et al. (1995), with increased taxon sampling and statistical support. The latest phylogeny for the Araceae (Cusimano et al., 2011) uses the same plastid regions as Cabrera et al. but slightly denser taxon sampling (113 genera, one accession per genus). Cusimano et al. also analyzed 81 morphological characters in the light of the plastid phylogeny and proposed a new formal classification of the Araceae. Tribe and subfamily names in the present thesis follow Cusimano et al. (2011).

Biogeography Araceae are distributed worldwide in habitats ranging from open freshwater to deserts. The majority of species occur in tropical rainforests. Except for the species-poor subfamilies Gymnostachydoideae, Orontioideae, and Zamioculcadoideae, with together 16 species in six genera, the five other subfamilies, which together contain 3289 species in 111 genera, are pantropically distributed. Genera and tribes tend to be endemic to particular continents, and only most genera of the free-floating Lemnoideae and *Pistia* have a worldwide distribution. Engler (1879, 1920), who was the first to summarize and discuss the global distribution of the Araceae family, was not able to explain the disjunctly distributed genera and tribes, and stated: "Sowohl die Verwandtschaftsverhältnisse der einzelnen Unterfamilien, der Tribus und Subtribus der Araceen wie auch die Tatsachen der geographischen Verbreitung weisen darauf hin, daß die gegenwärtige Verteilung der Kontinente wie auch die klimatischen Verhältnisse der Tertiärperiode nicht ausreichen, um die Verbreitung der einzelnen Unterfamilien zu erklären." (Engler, 1920, p. 50). The most recent analysis of Araceae biogeography is that of Mayo (1993). The most prominent disjunctions he discusses are in the genera that occur in tropical America and Southeast Asia; *Spathiphyllum* has 46 species in tropical America but also three in the Philippines, Sulawesi, and the Salomon Islands, and *Homalomena* has 69 species in tropical Asia and 13 in tropical America (Mayo et al., 1997; Croat and Boyce, 2012). Several groups discussed by Mayo have since been found not to be monophyletic. For instance, he thought *Schismatoglottis* represents a disjunct genus with 101 species in tropical Asia and three in tropical America, yet Wong et al. (2010) showed that the three neotropical species form a separate clade, the genus *Philonotion*. However, even in the light of the recent molecular phylogenies (French et al., 1995; Cabrera et al., 2008; Cusimano et al., 2011) many genera are still distributed across ocean barriers.

One prominent disjunction is that between the North American *Peltandra* (two species) and its sister genera *Typhonodorum*, *Arophyton*, *Carlephyton*, and *Colletogyne*, with together 12 species in Madagascar and East Africa (Croat and Boyce, 2012). Four genera span across the Bering Strait, *Arisaema* (205 species west and three species east of the Bering Strait), *Calla* (one species occurring on both sides), *Lysichiton* (1/1), and *Symplocarpus* (4/1) (Wen et al., 1996; Nie et al., 2006; Croat and Boyce, 2012). Seven genera reach from tropical Asia through the Malay Archipelago to Australia (*Alocasia*, *Epipremnum*, *Pothos*, *Remusatia*, *Rhaphidophora*, *Scindapsus*, and *Typhonium*), most of which have the majority of species in Southeast Asia and only few species in Australia (Mayo et al., 1997; Cusimano et al., 2010). Nine more genera (*Aglaonema*, *Amorphophallus*, *Amydrium*, *Cryptocoryne*, *Cyrtosperma*, *Homalomena*, *Lasia*, and *Schismatoglottis*) occur east and west of the Wallace Line without reaching Asia and Australia (Mayo et al., 1997; Cusimano et al., 2010; Croat and Boyce, 2012). Finally three genera occur in Africa and Asia; *Amorphophallus* has 42 in Africa and the Mascarene Islands and 153 species in Asia, *Rhaphidophora* has 97 species in Asia and six in Africa, and *Arisaema* has five species in Africa and the Arab Peninsula, 200 through tropical and temperate Asia, and further reaches with three species to the eastern part of North America, and one extending into Mexico (Renner et al., 2004; Croat and Boyce, 2012). Not taken into account in this list are single species with relatively wide distributions, which may have special adaptations for long-distance dispersal, like *Remusatia vivipara*, which has hooked bulbils that allow vegetative reproduction and may be easily dispersed by birds (Mayo et al., 1997).

Without the temporal framework from molecular clock dating, Engler and Mayo could not assess the roles of tectonic (geological) vicariance and long-distance dispersal as explanation for today's distribution ranges. Since Mayo's 1993 review, biogeographic analyses based on molecular phylogenetics and divergence dating have been performed for five subgroups of the Araceae; the *Pistia* clade (Renner and Zhang, 2004), *Arisaema* (Renner et al., 2004), Orontioideae (Nie et al., 2006), the Mediterranean Araceae (Mansion et al., 2008), and *Arum* (Espíndola et al., 2010). Two of these studies used fossil constraints placed at the crown node instead of the stem node of the relevant clade (Nie et al., 2006; Mansion et al., 2008); two studies constrained an artefactual node (involving *Alocasia* and *Colocasia*, as shown by my own work; Renner and Zhang, 2004; Mansion et al., 2008); and one, Renner et al. (2004), used a controversial fossil (*Arisaema hesperia*; Chapter 2, Supplementary Table 2) that was assigned relatively "distantly" in the phylogeny, resulting in old age estimates, that probably overestimate divergence times. Espíndola et al. (2010) used a secondary calibration based on the ages obtained by Mansion et al. (2008).

The rich fossil record of the Araceae family can provide insight into the minimal ages of particular clades as well as their past distribution at particular times. The oldest Araceae fossils date back to the Early Cretaceous (Friis et al., 2010), some subfamilies were already present in the Late Cretaceous, including the Orontioideae (Bogner et al., 2005, 2007), Lasioideae (Hofmann and Zetter, 2010), and Lemnoideae (Kvaček, 1995; Stockey et al., 1997), and several taxa are recorded from the Paleogene, e.g., *Montrichardia*, *Anthurium* (Herrera et al., 2008), the *Typhonodorum*-like forms, and Monstereae-like forms (Wilde et al., 2005). For a more detailed and complete list see Chapter 2, Supplementary Table 2. Fossils also sometimes come from locations far away from the distribution of their extant relatives, indicating past range shifts, e.g., monsteroid leaves from the Eocene of Germany (Wilde et al., 2005), and lasioid seeds from the Late Cretaceous of Siberia (Hofmann and Zetter, 2010). This information can be used to improve the ancestral area reconstruction.

The Malay Archipelago

A region of great interest for biogeographers is the Malay Archipelago with its high biodiversity, high levels of endemism, and complex geologic history (Wallace, 1863; Morley, 1998; Lohman et al., 2011). It covers a vast area between Asia and Australia, where since the end of the Oligocene the Indo-Australian, Pacific, and Eurasian tectonic plates collide, forming mountain chains and leading to the emergence and submergence of islands (Hall, 2002, 2009; Metcalfe, 2009). The geographic convergence of the Australian and Asian continents initiated the interchange of ancestrally Gondwanan and Laurasian lineages that dispersed into the newly available habitat. Aside from the geological factors, climatic changes had an important impact on the dispersal routes across the region, e.g., sea level fluctuations strongly impacted the exposed land area and connections between islands on the shallow continental shelves (Voris, 2000; Miller et al., 2005; Cannon et al., 2009).

In recent years the timing and directions of the floristic interchange of the region have been studied using molecular phylogenetics and divergence dating (Lohman et al., 2011; Richardson et al., 2012). Biogeographic studies of single clades using these methods are available for *Lithocarpus* (Cannon and Manos, 2003), *Macaranga* (Baenfer et al., 2006), the Meliaceae tribe Aglaieae (Muellner et al., 2008), the Annonaceae genus *Pseuduvaria* (Su and Saunders, 2009), the large genera *Cyrtandra* (Gesneriaceae; Clark et al., 2008) and *Begonia* (Begoniaceae; Thomas et al., 2011), and the palm genus *Livistona* (Arecaceae; Crisp et al., 2010). The predominant pattern in these groups is the colonization of the Malay Archipelago from west to east not earlier than the late Miocene.

A plant group that is species-rich in the Malaysian Archipelago and occurs on all major islands in the region as well as on the Asian and Australian continents is the Araceae genus *Alocasia*. I focus on this group to understand its actual distribution pattern in the context of the regions history, which itself will help to elucidate the biogeographic patterns shaping the high biodiversity of the Malay Archipelago.

The Genus *Alocasia*

Alocasia, with ca. 113 species including several awaiting description, is the 7^{th}-largest genus of the Araceae. It belongs to the *Pistia* clade in the Aroideae subfamily (Renner and Zhang, 2004; Cabrera et al., 2008; Cusimano et al., 2011) and is characterized by colocasioid venation (secondary lateral veins running parallel towards the leaf margin or forming a secondary collective vein) and wax glands in the axils of the primary lateral veins (Hay, 1998, 1999). *Alocasia* has been revised for Australasia (Hay and Wise, 1991), West Malesia and Sulawesi (Hay, 1998), the Philippines (Hay, 1998), and Thailand (Boyce, 2008).

Growth forms range from small herbs to massive, thick-stemmed plants with enormous leaves (see Chapter 3, Figure 2, or colorplate p.10). Several species have unusual leaf colors, from purple to metallic, with sometimes pale veins, making them interesting as ornamental plants. Two species have an additional value for man; *Alocasia cucullata* (Chinese taro) is an ethnobotanically important species cultivated on the Asian mainland in temples and used as totem plant in hilltribe villages in Lao PDR (Boyce, 2008), and *A. macrorrhizos* (giant taro) has edible tubers and leaves for which it is cultivated on some Oceanian islands (Weightman, 1989). Prior to my research, the wild origin of these two widely cultivated plants was unknown (Hay, 1999; Boyce, 2008).

Alocasia species are pollinated by drosophilid flies of the genus *Colocasiomyia*. Thermogenesis in the spadix (Ivancic et al., 2009) may help to attract the flies, which then mate and lay eggs at the basis of the inflorescence while they are protected and restrained by the spathe overnight and released with fresh pollen the following morning (Miyake and Yafuso, 2005; Sultana et al., 2006). Developing fruits, which are protected by the lower part of the spathe, turn orange to red when ripe and are dispersed by birds, e.g., of the genus *Pycnonotus* (P. C. Boyce; pers. comm., Nov. 2009). Little is known of hybridization in nature, but morphologically polymorphic species or species complexes have been suspected of involving hybridization (Hay, 1998, 1999). In cultivation, however, hybridization is common, even in distantly related species (Garner, 2010).

The natural range of *Alocasia* extends from India and Sri Lanka through Indochina to China and southern Japan, the Malay Archipelago, Oceania, and Australia. Its center of diversity lies on Borneo, where >40 species occur. The Asian mainland and the Philippines each host >20 species, New Guinea >15, Java, Sumatra and Sulawesi ca. 10, and Australia only one species. Almost all species are endemic to their region (island) and many have tightly restricted ranges, often associated with certain geology, e.g., limestone or granite; some are even considered as point endemics (occurring in only one location, e.g., *Alocasia pangeran* at the Madai Caves in Sabah, Malaysia, see colorplate p.10). The typical *Alocasia* habitat is the understory of perhumid lowland forests; only a few species grow above 1000 m altitude or in light-gaps, clearings, or secondary vegetation (Hay and Wise, 1991; Hay, 1998; Boyce, 2008).

Aim of this study

The aim of this thesis is to improve the understanding of the biogeographic history of the Araceae family in a global context and of the genus *Alocasia* in a regional one. The main questions that I address concern the ages and the ancestral areas of the respective lineages in order to reconstruct dispersal routes and to assess the role of dispersal and vicariance for the evolution of the focal groups. To this end, I produced molecular phylogenies to elucidate relationships and the evolutionary history of these taxa, performed divergence dating to gain the temporal context of diversification events, and reconstructed ancestral areas to understand past dispersal routes. For the whole family (Chapter 2), I use a phylogeny based on chloroplast DNA with at least one accession per genus and region, divergence dating relies on relaxed molecular clock methods with multiple fossil constraints, and biogeographic analyses including ancestral ranges and past dispersal routes in the DEC approach. For the genus *Alocasia* (Chapter 3), I compare chloroplast and nuclear phylogenies based on more than 70 ingroup accessions, perform divergence dating with strict and relaxed clock models and one fossil constraint, and reconstruct ancestral areas using parsimony and likelihood-based models without dispersal constraints.


Amorphophallus variabilis


Anthurium bakeri


Anthurium kallunkiae


Philodendron sp.


Alocasia lowii


Alocasia pangeran


Homalomena sp. nov.


Alocasia princeps


Alocasia robusta (red Sabah)

2

Araceae

Global history of the ancient monocot family Araceae inferred with models accounting for past continental positions and previous ranges based on fossils

Lars Nauheimer, Dirk Metzler, and Susanne S. Renner

New Phytologist

New Phytologist

Research

Global history of the ancient monocot family Araceae inferred with models accounting for past continental positions and previous ranges based on fossils

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Summary

- The family Araceae (3790 species, 117 genera) has one of the oldest fossil records among angiosperms. Ecologically, members of this family range from free-floating aquatics (*Pistia* and *Lemna*) to tropical epiphytes. Here, we infer some of the macroevolutionary processes that have led to the worldwide range of this family and test how the inclusion of fossil (formerly occupied) geographical ranges affects biogeographical reconstructions.
- Using a complete genus-level phylogeny from plastid sequences and outgroups representing the 13 other Alismatales families, we estimate divergence times by applying different clock models and reconstruct range shifts under different models of past continental connectivity, with or without the incorporation of fossil locations.
- Araceae began to diversify in the Early Cretaceous (when the breakup of Pangea was in its final stages), and all eight subfamilies existed before the K/T boundary. Early lineages persist in Laurasia, with several relatively recent entries into Africa, South America, South-East Asia and Australia.
- Water-associated habitats appear to be ancestral in the family, and DNA substitution rates are especially high in free-floating Araceae. Past distributions inferred when fossils are included differ in nontrivial ways from those without fossils. Our complete genus-level time-scale for the Araceae may prove to be useful for ecological and physiological studies.

Introduction

Molecular clocks calibrated with critically assessed fossils over the past 15 yr have provided major insights into plant evolution (e.g. Schneider *et al.*, 2004; Smith & Donoghue, 2008; Smith *et al.*, 2010; Clarke *et al.*, 2011; Crisp & Cook, 2011; Nagalingum *et al.*, 2011; for a review of earlier plant clock studies, see Renner, 2005). Because rate heterogeneity is a common occurrence in large datasets (Smith & Donoghue, 2008; Smith *et al.*, 2010), the introduction of relaxed molecular clock approaches presented a major advance for studies of macroevolution and biogeography (Sanderson, 1997, 2002; Thorne *et al.*, 1998; Drummond *et al.*, 2006; Himmelmann & Metzler, 2009). Nevertheless, challenges remain. The most important among them concern the handling of age constraints on calibration nodes (Yang & Rannala, 2006; Ho & Phillips, 2009; Clarke *et al.*, 2011; Wilkinson *et al.*, 2011) and how best to incorporate fossils (Manos *et al.*, 2007; Doyle & Endress, 2010). The latter topic is multi-facetted because fossils provide two kinds of information: the minimum age of a group and its presence in some geographical area at a specific time. It is this latter information that has proven difficult to incorporate into ancestral area reconstructions (AARs) (but see Clayton *et al.*, 2009).

Inferring past geographical ranges of plant clades is important if we are to understand the speed with which floras adapted to climate change *in situ* as opposed to the arrival of climatically pre-adapted lineages from other regions and the extinction of competitively inferior local lineages. Only large clades that occur in both temperate and tropical climates and that have a fossil record from different regions and geological eras are suitable for testing and improving the approaches available for the reconstruction of changing past ranges. Benchmark studies have focused on the tree family Simaroubaceae, the first plant group for which fossils were incorporated into a maximum likelihood (ML) biogeographical model (Clayton *et al.*, 2009), and the gymnosperm family Cupressaceae (Mao *et al.*, 2012). These are ancient (Jurassic to Cretaceous) families, and migration pathways available to them would have changed greatly after the breakup of Pangea and Gondwana, and more recent events, such as the closure of the Isthmus of Panama or the deterioration of the Beringian land bridge. Changes in connectivity between areas can be explicitly modelled using ML (Ree & Smith, 2008; Ree &

Sanmartín, 2009), and several studies have explored this option (Table 1).

Here, we use a complete genus-level phylogeny of the ancient monocot family Araceae to develop a synthetic approach that consists of, first, the evaluation of the sensitivity of time inference to different implementations of prior constraints on node ages and, second, the modelling of the changing continental connections through time and the incorporation of the best-supported fossils *directly* into AARs. We compare the results obtained with and without information on past (no longer occupied) ranges to arrive at a plausible scenario for the earliest history of Araceae. The family Araceae comprises 3790 species in 117 genera (Boyce & Croat, 2011). They are among the horticulturally most important families of monocotyledons and have received much attention from pollination ecologists (Chouteau *et al.*, 2008). Although the family Araceae is most diverse in the tropics, it includes a few genera in the subtropics and temperate regions of North America, Eurasia, the Mediterranean region and Australia that occur in habitats ranging from bogs to deserts (Fig. 1). Molecular and morphological phylogenetic analyses have included representatives of most of the genera (Cabrera *et al.*, 2008; Cusimano *et al.*, 2011). A formal biogeographical analysis, however, has never been attempted, and a review of the family's biogeography was premolecular and, in hindsight, interpreted many unnatural groups (Mayo, 1993).

There is no doubt that members of the family Araceae were geographically widespread in the Cretaceous (Stockey *et al.*, 1997, 2007; Friis *et al.*, 2004, 2006, 2010; Bogner *et al.*, 2005, 2007; Wilde *et al.*, 2005; Herrera *et al.*, 2008). The quality of several of their fossils not only allows the robust calibration of DNA substitution rates, but, importantly, also provides information about past ranges of certain clades. We used this fossil record in Bayesian analyses with relaxed molecular clock models and biogeographical likelihood analyses. Our primary questions are as follows: when and where did the family Araceae undergo its early diversification?; what is the geographical and temporal context of the family's two aquatic lineages (*Pistia*, Lemnoideae)?; and what has been the impact on Araceae of the climate change from the Palaeocene/Eocene high temperatures to the Oligocene and Miocene cooling?

Materials and Methods

Sampling and alignment of DNA

We augmented the datasets of Cabrera *et al.* (2008) and Cusimano *et al.* (2011) by sequencing from disjunctly distributed or newly described genera, namely *Alocasia*, *Amorphophallus*, *Apoballis*, *Arisaema*, *Colocasia*, *Hestia*, *Homalomena*, *Nephthytis*, *Ooia*, *Pichinia* and *Rhaphidophora*. The final alignment comprised 132 Araceae plus *Acorus* (Acoreaceae), sister to all other monocots, and *Tofieldia* (Tofieldiaceae), to represent the sister clade of the Araceae (Supporting Information Table S1 provides species, author names, herbarium voucher information and GenBank accession numbers).

Table 1 Biogeographical studies that have used maximum likelihood models with constrained dispersal probabilities and the ways in which they have accommodated uncertainty

Authors	Root age (Ma)	Number of tips	Number of areas	Number of time slices	Comparison with equal dispersal null model	Comparison of dispersal probability models	Comparison of time-slice models	Comparison with DIVA	Fossil ranges included[1]	Statistical evaluation (# of AARs)	Using several input chronograms
Clayton *et al.* (2009)	70	49	7	4	No	No	No	Yes	Yes, a	No	No
Smith (2009)	60	92	4	2	Yes	No	No	No	No	Yes (1500)	No
Bouchenak-Khelladi *et al.* (2010)	60	161	4	5	Yes	No	No	No	No	No	No
Buerki *et al.* (2011)	130	169	7	4	Yes	No	No	Yes	No	No	Yes
Salvo *et al.* (2010)	32.5	48	15	7	No	No	No	No	No	No	Yes
Couvreur *et al.* (2011)	100	98	7	5	Yes	Yes	No	No	No	No	No
Fernández-Mazuecos & Vargas (2011)	8	34	4	3	Yes	No	No	Yes	No	Yes (100)	No
Valente *et al.* (2011)	30	150	5	1	Yes	No	No	No	No	No	No
Appelhans *et al.* (2012)	75	40	8	4	No	No	No	No	No	No	No
Carlson *et al.* (2012)	70	29	3	5	Yes	No	No	No	No	No	No
Santos-Gally *et al.* (2012)	25	41	4	6	Yes	No	No	No	No	No	No
Mao *et al.* (2012)	225	122	6	0–8	No	No	Yes	No	Yes, a	No	No
This study	150	145	8	3,4	No	No	Yes	No	Yes, a + b	No	No

AAR, ancestral area reconstruction; DIVA, dispersal vicariance analysis (Ronquist, 1997).

[1] a, fossils include on long branches, simulating ranges occupied until now; b, fossils included on short branches, simulating extinct ranges.

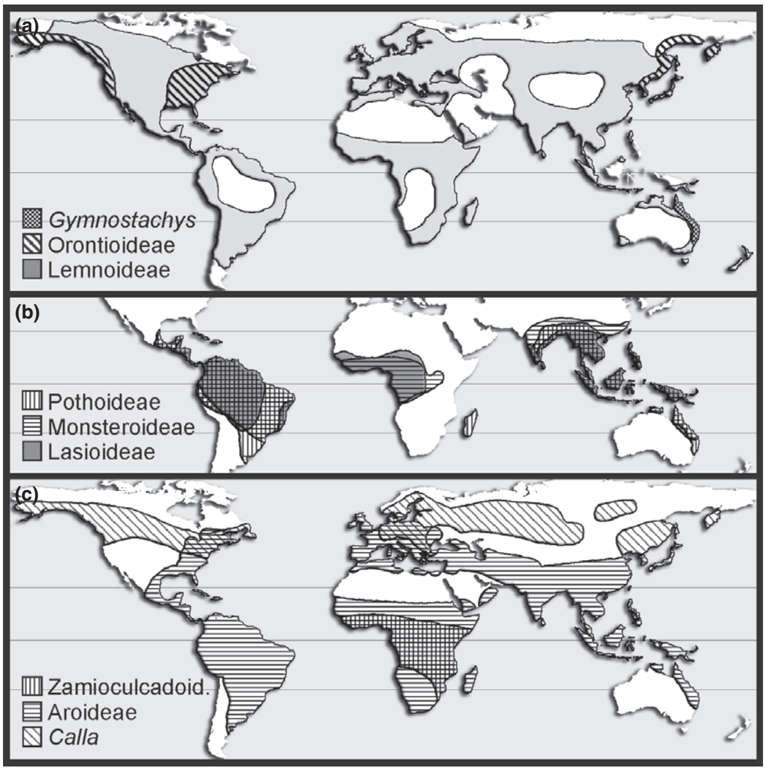


Fig. 1 Distribution maps of the eight subfamilies of Araceae: (a) Gymnostachydoideae, Orontioideae and Lemnoideae; (b) Pothoideae, Monsteroideae and Lasioideae; (c) Zamioculcadoideae, Aroideae without *Calla* and only *Calla*.

Like previous family-wide analyses, we relied on chloroplast loci, namely the *trnL* intron and spacer, the *matK* gene and partial *trnK* intron, and the *rbcL* gene. We used standard primers, except for *matK* for which we used the Araceae-adapted primers of Cusimano *et al.* (2010). Sequences were edited and aligned manually using Sequencher 4.7, and regions of uncertain alignment were excluded, leading to the removal of 881 nucleotides, mostly as a result of several autapomorphic indels and microsatellite regions in the *trnL* intron. The final matrix included 4343 aligned positions, 2987 of which belonged to coding regions; it was deposited in TreeBASE (submission 12268).

Phylogenetics and relaxed molecular clock dating

Phylogenetic analyses of the concatenated sequence data were performed under ML optimization, using RAxML 7.2.6 (Stamatakis *et al.*, 2008) with separate GTR + Γ substitution models for coding and noncoding regions, and the fast bootstrap option, using 1000 replicates. Throughout this article, > 85% bootstrap support (BS) is considered as medium support and 95–100% as strong support. Chronograms (phylogenies with branch lengths scaled to geological time) were estimated using two Bayesian methods: TreeTime (Himmelmann & Metzler, 2009) and BEAST (Drummond *et al.*, 2006, 2012; Drummond & Rambaut, 2007).

In BEAST (versions 1.6.2 and 1.7.0), rate variation across branches is modelled as uncorrelated and log-normally distributed. We used a pure birth (Yule) tree prior and the substitution models recommended by jModeltest: TPM1uf + Γ for the noncoding region and GTR + Γ for the coding region taking into account codon positions. An additional analysis applied the simpler JC + Γ substitution model to assess possible overparameterization. We ran 12 × 20 million generations of Monte Carlo Markov chains (MCMC) for the more complex substitution model and 6 × 15 million generations for the simple model. Convergence was analysed in Tracer (1.5; Rambaut & Drummond, 2007), and runs were continued until effective sample sizes (ESSs) were > 200. Separate runs reached similar posterior probabilities (PPs) and, after the exclusion of appropriate burn-in fractions, they were concatenated in LogCombiner (1.6.2, part of the BEAST package) and resampled at a lower density to obtain a final sample of *c.* 10 000 trees. Maximum clade credibility trees with mean node heights were constructed using TreeAnnotator (1.6.2, part of the BEAST package). We also ran analyses with empty alignments (‘prior-only’ option), and compared the resulting posterior divergence times to assess the influence of prior settings.

Nodes with PP ≥ 0.95 were considered to be moderately well supported and nodes with PP = 1 as strongly supported.

TreeTime (version 1.0.1; http://evol.bio.lmu.de/_statgen/software/treetime/) differs from BEAST in not using a tree prior and, instead, assuming a uniform prior for all combinations of branch lengths, conditioned on the exponentially distributed age of the root and the additional priors for node ages, as specified by the user for time calibration. The user can choose among four models of rate change along the tree, a compound Poisson distribution, a Dirichlet distribution, an uncorrelated exponential distribution (UCED) or an uncorrelated log-normal distribution, but there is no statistical way to select the best-fitting model for one's data. We therefore ran all four models, always using the GTR + Γ substitution model and 2×5 MCMC of one million generations, with a burn-in period of 10 000 generations and parameters sampled every 1000th tree. Results from two runs per rate change model were combined manually to create an input file for TreeAnnotator in which the maximum clade credibility tree with mean node heights was then obtained.

Fossil calibration

Table S2 lists all fossils, with the morphological arguments for their attribution to Araceae or particular nodes within that family. Of the 21 fossils, we used seven for calibration purposes and nine in the geographical analyses of past ranges (see the next section). For absolute ages, we relied on the time-scales of Walker & Geissman (2009) and Ogg (2010).

(1) The subfamily Orontioideae is represented by macrofossils from the Late Cretaceous to the Eocene of North America and Europe (Bogner *et al.*, 2005, 2007). A fossilized infructescence (*Albertarum pueri*) from Alberta, Canada, provides a minimum constraint of 72 million years ago (Ma) for the stem node of Orontioideae (node 3 in all figures and table). Slightly younger fossils of Orontioideae are *Lysichiton austriacus*, *Orontium mackii*, *O. wolfei* and *Symplocarpus hoffmaniae* (Table S2). (2) The subfamily Lasioideae is first known from the pollen taxon *Lasioideaecidites* from the Late Cretaceous of Siberia (Hofmann & Zetter, 2010; Table S2), and we used the age of *L. hessei* (70 Ma) to constrain the stem lineage (node 28). (3) The oldest free-floating member of Araceae is represented by *Limnobiophyllum scutatum* from the Late Cretaceous of North America (a taxon occurring into the Oligocene in East Asia). We used the oldest occurrence of *L. scutatum* (65.5 Ma; Kvacek, 1995; Table S2) to constrain the stem lineage of Lemnoideae (node 6). (4) The subfamily Aroideae is first known from the Palaeocene Colombian leaf taxon *Montrichardia aquatica* (Herrera *et al.*, 2008; Table S2), and we used the age of this fossil (55.8 Ma) to constrain the stem node of *Montrichardia* (node 44). (5) The same formation also contains fossil leaves resembling those of the living genus *Anthurium* (Herrera *et al.*, 2008), and we used the age of *Petrocardium cerrejonense* (55.8 Ma) to constrain the stem node of *Anthurium* (node 13). (6) The *Typhonodorum* clade (see the Results section, Fig. 2) is first represented by the leaf morphogenus *Nitophyllites*, with *N. zaisanicus* from the Palaeocene (55.8 Ma) of Kazakhstan (Wilde *et al.*, 2005), *N. limnestis* from the middle Eocene of America (Dilcher & Daghlian, 1977; Wilde *et al.*, 2005) and *N. bohemicus* from the lower Eocene of the Czech Republic (Wilde *et al.*, 2005). We used an age of 55.8 Ma to constrain the stem node of the *Typhonodorum* clade (node 62). (7) The subfamily Monsteroideae is first known from the leaf fossil *Araciphyllites tertiarius* from the middle Eocene (47 Ma) of Germany (Wilde *et al.*, 2005). Monsteroid leaves, however, evolved at least twice in the Araceae, once in the New World *Heteropsis* clade and once in the Old World *Rhaphidophora* clade (Cusimano *et al.*, 2011; see the Results section, Fig. 2). The German leaves closely resemble those of living Asian species in the genera *Epipremnum*, *Rhaphidophora* and *Scindapsus*, arguing for an assignment to the stem lineage of these Old World genera. We therefore used 47 Ma to constrain the stem lineage of the *Rhaphidophora* clade (node 20). (8) Our constraint for the root (the monocot crown node) is based on the oldest monocot pollen (*Liliacidites*, 125 Ma; Doyle *et al.*, 2008; Table S2) as the minimum boundary combined with the youngest (139 Ma) and oldest (138 Ma) median ages inferred for the monocot crown group in molecular clock studies (Bell *et al.*, 2010; Smith *et al.*, 2010). The 125- or 112-Ma pollen taxon *Mayoa portugallica* (Friis *et al.*, 2004, 2010; Table S2) may also represent Araceae, but the exine structure of *Mayoa* is 'rarely columellae-like' (Friis *et al.*, 2004: 16 566), raising the possibility that the grain might be from a gymnosperm (Hofmann & Zetter, 2010). Inflorescences including *in situ* pollen from the Albian/Aptian of Portugal (112 Ma; Table S2) clearly represent Araceae (Friis *et al.*, 2010), but cannot yet be confidently assigned to particular nodes.

Using the above fossils, we devised two prior constraint schemes. The first consisted of uniform priors with hard minimum bounds for the seven fossils and a normal distribution with a soft minimum and maximum bound for the root (mean, 132 Ma; standard deviation, 4.25 Ma). The maximum bound on the uniform priors was set to 500 Ma, an age sufficiently high to effectively give all possible ages up to the soft maximum constraint at the root an equal probability. The second scheme consisted of gamma-distributed priors for all eight constraints, resulting in a higher probability (compared with the uniform priors) of ages falling close to the minimum constraint. For the root, our gamma distribution had an offset of 123.9, a shape parameter of 2 and a scale parameter of 3.07, which permitted 5% of the inferred ages to be < 125 Ma, 5% to be > 138.5 Ma, with 90% falling in between these two dates (based on the same rationale as above, constraint 8). For the remaining seven fossils, we chose gamma distributions with shape parameters 2 and offsets and scales set so that 5% of the ages could be younger than the respective fossil and 5% could be older than the earliest monocot pollen, *Liliacidites*.

Four earlier studies have dated groups of Araceae using fossil calibrations. Nie *et al.* (2006) used *Albertarum puerii* (72 Ma; our constraint 1) as a minimum constraint for the six species of Orontioideae living today, whereas we place this fossil at the relevant stem node. Renner & Zhang (2004) and Mansion *et al.* (2008) assigned *Nitophyllites zaisanicus* (our constraint 6) to the split between *Typhonodorum* and *Peltandra*, whereas we assign this fossil to the stem of this clade. They also assigned a 45-Ma leaf fossil, *Caladiosoma messelense* (Wilde *et al.*, 2005), to an apparent *Alocasia/Colocasia* node, since shown to have been an artefact (Nauheimer *et al.*, 2012). Lastly, Renner *et al.* (2004a) used a controversial fossil from the Miocene Latah Formation near Spokane (16–18 Ma) to constrain the split between *Arisaema triphyllum* from North America and *A. amurense* from Korea, China and Russia (Renner *et al.*, 2004b), resulting in relatively old ages inferred for that genus.

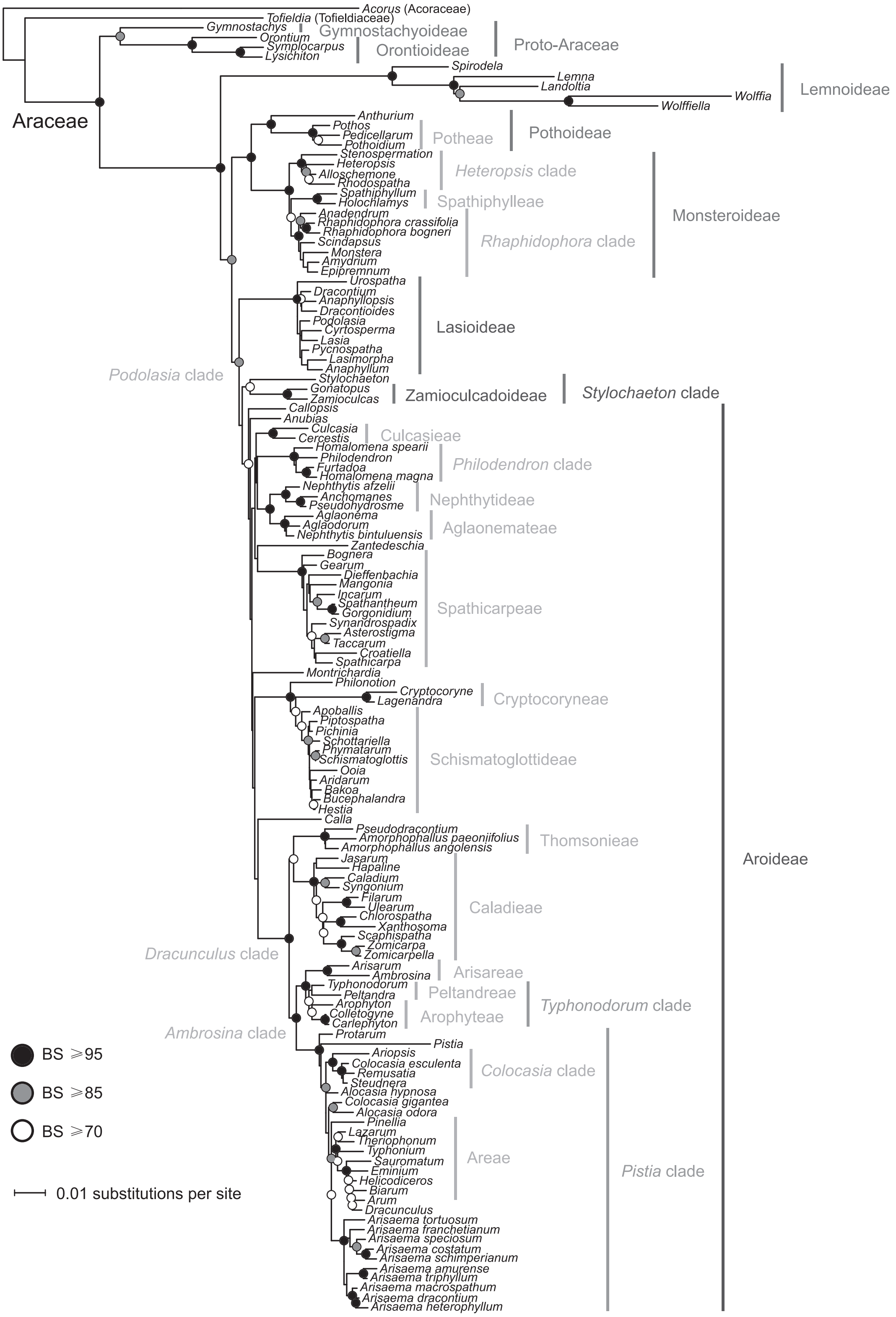
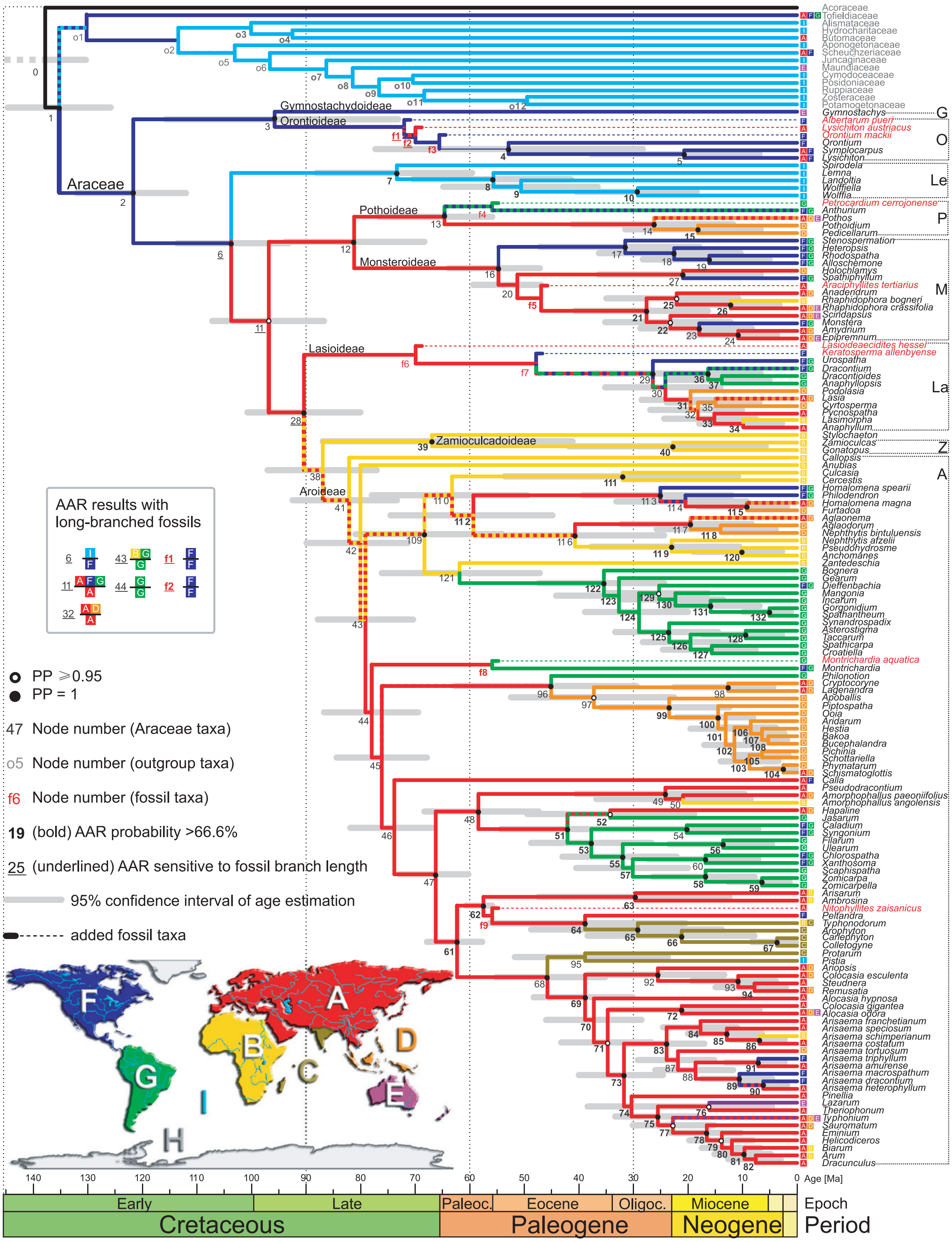


Fig. 2 Maximum likelihood tree for the Araceae based on 4343 aligned nucleotides of plastid DNA. Support values based on 1000 bootstrap replicates are indicated by the circles at the nodes: white ≥ 70, grey ≥ 85 and black ≥ 95%. Clade names follow Cusimano *et al.* (2011).


Acoraceae
Tofieldiaceae
Alismataceae
Hydrocharitaceae
Butomaceae
Aponogetonaceae
Scheuchzeriaceae
Juncaginaceae
Maundiaceae
Cymodoceaceae
Posidoniaceae
Ruppiaceae
Zosteraceae
Potamogetonaceae
Gymnostachys
Albertarum pueri
Lysichiton austriacus
Orontium mackii
Orontium
Symplocarpus
Lysichiton
Spirodela
Lemna
Landoltia
Wolffiella
Wolffia
Petrocardium cerrojonense
Anthurium
Pothos
Pothoidium
Pedicellarum
Stenospermation
Heteropsis
Rhodospatha
Alloschemone
Holochlamys
Spathiphyllum
Araciphyllites tertiarius
Anadendrum
Rhaphidophora bogneri
Rhaphidophora crassifolia
Scindapsus
Monstera
Amydrium
Epipremnum
Lasioideaecidites hesseі
Keratosperma allenbyense
Urospatha
Dracontium
Dracontioides
Anaphyllopsis
Podolasia
Lasia
Cyrtosperma
Pycnospatha
Lasimorpha
Anaphyllum
Stylochaeton
Zamioculcas
Gonatopus
Callopsis
Anubias
Culcasia
Cercestis
Homalomena spearii
Philodendron
Homalomena magna
Furtadoa
Aglaonema
Aglaodorum
Nephthytis bintuluensis
Nephthytis afzelii
Pseudohydrosme
Anchomanes
Zantedeschia
Bognera
Gearum
Dieffenbachia
Mangonia
Incarum
Gorgonidium
Spathantheum
Synandrospadix
Asterostigma
Taccarum
Spathicarpa
Croatiella
Montrichardia aquatica
Montrichardia
Philonotion
Cryptocoryne
Lagenandra
Apoballis
Piptospatha
Ooia
Aridarum
Hestia
Bakoa
Bucephalandra
Pichinia
Schottariella
Phymatarum
Schismatoglottis
Calla
Pseudodracontium
Amorphophallus paeoniifolius
Amorphophallus angolensis
Hapaline
Jasarum
Caladium
Syngonium
Filarum
Ulearum
Chlorospatha
Xanthosoma
Scaphispatha
Zomicarpa
Zomicarpella
Arisarum
Ambrosina
Nitophyllites zaisanicus
Peltandra
Typhonodorum
Arophyton
Carlephyton
Colletogyne
Protarum
Pistia
Ariopsis
Colocasia esculenta
Steudnera
Remusatia
Alocasia hypnosa
Colocasia gigantea
Alocasia odora
Arisaema franchetianum
Arisaema speciosum
Arisaema schimperianum
Arisaema costatum
Arisaema tortuosum
Arisaema triphyllum
Arisaema amurense
Arisaema macrospathum
Arisaema dracontium
Arisaema heterophyllum
Pinellia
Lazarum
Theriophonum
Typhonium
Sauromatum
Eminium
Helicodiceros
Biarum
Arum
Dracunculus
G
O
Le
P
M
La
Z
A
Araceae
Gymnostachydoideae
Orontioideae
Pothoideae
Monsteroideae
Lasioideae
Zamioculcadoideae
Aroideae
AAR results with long-branched fossils
PP ⩾0.95
PP = 1
47 Node number (Araceae taxa)
o5 Node number (outgroup taxa)
f6 Node number (fossil taxa)
19 (bold) AAR probability >66.6%
25 (underlined) AAR sensitive to fossil branch length
95% confidence interval of age estimation
added fossil taxa
F
G
I
B
A
C
D
E
H
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
Age [Ma]
Early
Late
Paleoc.
Eocene
Oligoc.
Miocene
Epoch
Cretaceous
Paleogene
Neogene
Period

Biogeographical analyses

For AARs, we relied on the dispersal–extinction–cladogenesis (DEC) model, implemented in Lagrange (Ree *et al.*, 2005; Ree & Smith, 2008). It uses the information contained in genetic branch lengths and allows the incorporation of changing dispersal probabilities across areas and time. We devised two time-slice models, one with bins of 0–30, 30–90 and 90–150 Ma, and the other with bins of 0–30, 30–60, 60–90 and 90–150 Ma (Table S3). The oldest bin captures the plate tectonic situation before the breakup of West Gondwana, and the youngest the period during which the Central American land bridge and South-East Asia formed. The middle bins tried to capture connectivity via the North Atlantic land bridge and Antarctica, and differed in the way in which India connects to Eurasia (Table S3). Our nine operational geographical units were Eurasia (A), Africa (B), Madagascar (C), South-East Asia and India (D), Australia (E), North and Central America (F), South America (G) and Antarctica (H). To accommodate the mostly globally distributed water-associated and free-floating taxa, we created a ninth category, 'water-associated' (I), assigned to the marine Alismatales families Cymodoceaceae, Posidoniaceae, Ruppiaceae and Zosteraceae, the freshwater aquatics Alismataceae, Aponogetonaceae and Potamogetonaceae, plants of marshy coastal habitats (Juncaginaceae), and free-floating Araceae (Lemnoideae, *Pistia*). *Remusatia* was coded as present only in area D because most of its species occur in the Himalayan foothills and the Western Ghats of India; the widespread *R. vivipara*, occurring in Africa, Asia and Australia, is especially adapted to bird dispersal. Similarly, *Pothos*, occurring on Madagascar with one widespread species (*P. scandens*), was only coded for areas A, D and E, where it has several species, and *Sauromatum* was only coded for areas A and D, although it also has one species (*S. venosum*) ranging from Africa to tropical China. *Spathiphyllum* was coded for South America and Central North America, where 44 species occur, but not for South-East Asia, where *S. commutatum* and *S. solomonense* occur on the Philippines and New Guinea; its monospecific sister group, *Holochlamys*, is endemic on New Guinea. In the absence of molecular phylogenetic evidence on the relationships of the two Asian *Spathiphyllum* species, we felt it unwise to code this genus as present in Asia because its two Asian species may turn out instead to belong to *Holochlamys*.

To create a tree that included all families of Alismatales (the order to which the Araceae family belongs), we manually added one representative per family to a newick tree file obtained from BEAST. The topology and divergence times were constrained to match the results of the large monocot chronogram of Janssen & Bremer (2004). The enlarged tree had 145 tips (132 Araceae and 13 outgroups) and became the input tree for Lagrange. To create Python script input files (with the tree of choice and the area connectivity probability matrices; Table S3), we used the Lagrange online configurator tool. Ancestral areas were limited to maximally two, and a relative probability of > 66.6% was considered to be strong support for an ancestral range scenario.

To integrate fossil ranges into the reconstructions, we added them manually in the newick chronogram (as performed for the Alismatales outgroups, above). Each fossil was inserted along the stem lineage of the group to which it had been assigned, with its age determining where it was placed. In addition, each fossil was given either a short branch length (1 Ma), simulating an extinct range, or a long branch length (the fossil's age), simulating a range occupied for a long time (until today). When fossils are given short branch lengths, the DEC model, which considers branch lengths as proportional to time, will treat any range shifts indicated by their geographical occurrences as evidence for rapid geographical change (and, conversely, for long branch lengths). One of the seven fossils used for clock calibration, *Limnobiophyllum scutatum*, was not used in the AAR because it was too young to be assigned to the relevant stem lineage, whereas three others that had not been used as constraints were added because they contributed geographical information (*Lysichiton austriacus*, *Orontium mackeii* and *Keratosperma allenbyense*; Table S2).

Results

Ages and substitution rates inferred using different clock models and calibration priors

Results from BEAST runs with an empty alignment revealed no contradictions among the prior constraints and showed that the PPs with the complete alignment differed from those without, indicating that the signal in the data overwrote the priors. The topologies of the ML phylogeny (Fig. 2) and the Bayesian relaxed clock chronograms (Figs 3, S2) differ only in the placement of a few statistically unsupported nodes. Although the testing of generic boundaries is not the topic of this study, four of the seven genera for which we included more than one species turned out to be polyphyletic. The Bornean species of *Nephthytis* (*N. bintuluensis*) groups with other South-East Asian genera, and

Fig. 3 Results from divergence dating with BEAST and ancestral area reconstruction (AAR) with fossils included and assigned short branch lengths. Grey bars at nodes show 95% confidence intervals. Exact ages are shown in Supporting Information Table S5. Black dots with a white centre indicate a posterior probability (PP) of ≥ 0.95, entire black dots PP = 1. Araceae taxon names are in black, outgroup names in grey and added fossil taxa in red. Branches are coloured by area: Eurasia in red (A), Africa in yellow (B), Madagascar in ochre (C), South-East Asia and India in orange (D), Australia in purple (E), North America in dark blue (F), South America in green (G), Antarctica in grey (H) and world-wide-distributed water-associated taxa in turquoise (I). Letters to the left of taxon names show the area coded for that taxon. Only the AAR with the highest probability is shown; those with bold numbers have a probability ≥ 66.6%. Underlined node numbers mark nodes sensitive to whether fossils were given long or short branches. Letters in boxes next to taxon names indicate subfamilies: Gymnostachydoideae (G), Orontioideae (O), Lemnoideae (Le), Pothoideae (P), Monsteroideae (M), Lasioideae (La), Zamioculcadoideae (Z), Aroideae (A).

the African type species of the genus (*N. afzelii*) groups with other African genera (nodes 118 and 119). The Asian representative of the large genus *Homalomena* groups with another Asian genus (*Furtadoa*), and both are sister to the American genus *Philodendron*, whereas the sampled American species of *Homalomena*, which has few species on that continent, falls elsewhere (nodes 113 and 115). The Asian genera *Alocasia* and *Colocasia* are also polyphyletic (nodes 70, 72, 93).

Combining independent Bayesian MCMCs yielded ESSs > 200, indicating that the posterior estimates were not unduly influenced by autocorrelation. The parameter-intensive complex substitution model needed > 200 million MCMC generations to reach the > 200 ESS threshold, whereas the simple model needed 50 million. Ages for statistically supported nodes in the resulting chronograms under complex or simple substitution models differed by only 4.1% on average (Table S4).

The ages obtained from the TreeTime analyses using the compound Poisson process, the Dirichlet model, UCED or an uncorrelated log-normal distribution are shown in Table S4. The root node (monocot crown group) was between 204 and 146 Ma, but these drastic differences did not consistently carry through to the tips. TreeTime differs from BEAST in using no tree prior and instead assuming a uniform prior for all combinations of branch lengths, conditioned on the exponentially distributed age of the root and the additional priors specified by the user for time calibration. This may be the reason for the generally older root ages in TreeTime, whereas the ages higher up in the tree were not that different from those obtained with BEAST (Table S4). We know of no statistic for choosing among the four models in TreeTime, but note that the UCED model yielded ages closest to those from BEAST. Below, we focus on the BEAST chronogram from the constraint scheme using the uniform priors for the seven fossils and the simple substitution model, rather than the chronogram obtained with the gamma priors and complex substitution models (all results are shown in Table S4).

With BEAST, the Araceae stem lineage (Fig. 3, node 1) is dated to 135 Ma and the Araceae crown group (node 2) to 121.7 Ma (95% confidence intervals (CIs) on all ages are shown in Table S4). Six of the eight subfamilies (marked with capital letters in Fig. 3) existed by the Late Cretaceous (*c.* 100–80 Ma), the Lemnoideae even a bit earlier (103.6 Ma); the Zamioculcadoideae evolved just around the K/T boundary (67 Ma). The crown groups of most subfamilies are much younger than their stems, most extremely so in the Lasioideae (stem, 90 Ma; crown, 26 Ma). By contrast, the most species-rich subfamily, the Aroideae (1573 species in 75 genera), diversified into 10 major lineages between 87 Ma (node 38) and 62.3 Ma (node 61).

The posterior age distributions (Fig. S3) obtained for three of the constrained nodes are substantially shaped by their priors *Nitophyllites zaisanicus* (estimated mean 57.5 Ma/constrained 55.8 Ma), *Araciphyllites tertiarius* (51.38 Ma/47 Ma) and *Petrocardium cerrejonense* (64.51 Ma/55.8 Ma), whereas the fossils *Lasioideaecidites hessei*, *Limnobiophyllum scutatum* and *Montrichardia aquatica* hardly affected the posterior distribution of the nodes to which they were assigned.

Plastid DNA substitution rates across the Araceae vary from values of 1.23×10^{-4} to 2.19×10^{-3} substitutions per site per million years (Table S5, Fig. S1). The average rate is 4.12×10^{-4} and the median 3.47×10^{-4}. The highest rates ($> 10^{-3}$) occur on branches leading to the free-floating Lemnoideae and *Pistia*, the stem of the aquatic *Cryptocoryne* and *Lagenandra*, and the branches between nodes 2 and 6.

Ancestral areas inferred with and without information from fossil ranges

We ran AARs with each of the two time-slice models and compared the resulting global likelihoods; the three-time-slice model (Table S3) resulted in a higher likelihood than the four-time-slice model and was therefore preferred. The ancestral areas inferred with ancient ranges (from fossils) included and assigned short branches are shown in Fig. 3; those inferred from only the geographical ranges of living genera are shown in Fig. S2. Nodes that changed when fossils were given long branches are shown in the inset in Fig. 3. The probabilities for ancestral areas obtained with the three fossil insertion models are given in Table S5. The inferred ancestral areas for most of the 131 ingroup nodes had probabilities of > 66.6%.

The inclusion of fossil ranges in the AARs had the greatest effects in early-diverging lineages and in nodes close to fossils. Without fossil ranges, the origin of the Araceae (node 1), its first divergence (node 2) and the Gymnostachydoideae lineage (node 3) are reconstructed as water associated. With fossil ranges included, these lineages are reconstructed as originating in West Laurasia (North America). Whether fossils were simulated as extinct lineages by giving them short branches or as still living lineages by giving them long branches affected seven aroid nodes (Fig. 3, inset; Table S5). For example, node 44 is inferred as having Asian descendants in the short-branched model, but South American ones in the long-branched model. The short-branch model may be more realistic as these fossil lineages obviously no longer occupy their former ranges.

A striking geographical disjunction in the Aroideae involves *Hapaline* (node 52; seven species), the only Asian member of an otherwise South American clade (its sister group is the monotypic South American genus *Jasarum*). This divergence apparently dates to the Eocene/Oligocene boundary at 34 Ma (19–49 Ma). A similarly unusual disjunction is that between *Peltandra*, with two species in Florida and the eastern USA, and its closest relatives (*Typhonodorum* and three other genera) in East Africa, Madagascar and adjacent islands (Mayo, 1993; our Fig. 3, node 64). AARs with or without fossil ranges (nodes 62 and f9) infer a Eurasian origin of the stem lineage of this clade (Madagascar then probably reached by over-water dispersal from Africa or Asia). Another case of apparent trans-oceanic dispersal involves node 27, the Monsteroideae genus *Spathiphyllum*, with 44 species in Central and South America, two on the Philippines and New Guinea (not sequenced), and *Holochlamys*, with a single species in New Guinea. This split is dated to 21 Ma (7–36 Ma) and, according to our AARs, is a result of trans-Laurasian range expansion (Fig. S2). This inference should probably be viewed sceptically because of the incomplete sampling of the relevant species.

Discussion

This study provides the first complete genus-level chronogram for the Araceae and a biogeographical analysis that not only incorporates formerly occupied ranges but also treats the incorporated fossils in different ways and tests the fit of different time-slice models. Table 1 summarizes the methodological progress in AARs over the past few years and shows how our study differs from previous approaches. The point of including fossils on short or long 'genetic' branches was to simulate fossil lineages that either went extinct shortly after the age of the respective fossil or that persisted for a long time. The primary questions we wished to answer in this study were when and where the Araceae family underwent its early diversification, the time of evolution of the family's two aquatic lineages (*Pistia*, Lemnoideae) and the impact of the climate change over the past 60 million years. The answers to these questions are provided in the three Discussion sections below. We also briefly discuss the unexpectedly high substitution rates in aquatic Araceae.

All AAR hinges on the correct inference of time. We therefore inferred divergence times using different approaches. The TreeTime program (Himmelmann & Metzler, 2009) yielded surprisingly older root ages than obtained with BEAST, whereas ages near the tips inferred from the two approaches were in better agreement, especially under the UCED model (Table S4). The two programs differ in using a tree prior (BEAST) or not (TreeTime), and this may affect root ages. BEAST runs carried out with simple or complex substitution models, and using gamma distributions or uniform distributions on the fossil prior constrains, yielded similar node ages (Table S4), the main difference being that results were obtained much more quickly with the simpler models.

Different approaches have been used to assess the effect of chronogram uncertainty on AARs (Smith, 2009; Salvo *et al.*, 2010; Buerki *et al.*, 2011; Fernández-Mazuecos & Vargas, 2011; our Table 1); basically, ancestral areas were inferred on many chronograms, rather than just one. Because of the size of our tree and the complexity of manually adding the fossils, we refrained from using one of the TreeTime chronograms as input for an AAR, but instead relied on the BEAST chronogram obtained with uniform prior constraints, which we feel is the most conservative dating approach.

A further methodological issue is how one should choose among different time-slice models. We compared the global likelihood of models that assumed different area connectivity in three or four time bins (0–30, 30–90, 90–150 Ma or 0–30, 30–60, 60–90, 90–150 Ma; Table S3), and preferred the three-time-slice model because it had a higher likelihood. The only other study to compare the fit of different time slices (Mao *et al.*, 2012; our Table 1) found that a more complex time-slice model fitted their data better than a simpler one, but it is not completely clear what metric to use to assess model fitting (R. Ree, Field Museum, Chicago, IL, USA, pers. comm., March 2012).

Araceae in time and space – early occupation of aquatic habitats

At the onset of the Early Cretaceous, when the Araceae diverged from the remaining Alismatales (138 Ma; CI, 130–146 Ma), the breakup of Pangea (160–138 Ma) into the supercontinents Laurasia and Gondwana was essentially complete. North America and South America, however, were still close (Smith *et al.*, 2004). The inferred origin of the Araceae as 'water associated' (without the benefit of fossil range information) or Laurasian (with fossils included and assigned short or long branches) matches several lines of evidence.

An origin in wet habitats fits the ecology of, and fossils associated with, early-diverging clades in the family. The deepest divergence in Araceae is between a clade comprising the Australian subfamily Gymnostachydoideae (one species) and the North American and Asian subfamily Orontioideae (seven species) plus their sister clade comprising the remaining six subfamilies of Araceae. This divergence dates to *c.* 122 Ma (CI, 112–132 Ma; node 2 in all figures and tables). All living gymnostachyoid/orontioid species are restricted to wet habitats (Bogner *et al.*, 2007). Next-oldest divergences involve the entirely aquatic Lemnoideae, dating to *c.* 104 Ma (CI, 93–113 Ma; node 6), and the split between the Australian *Gymnostachys* and the Northern Hemisphere orontioids, dating to *c.* 96 Ma (CI, 73–115 Ma; node 3). Considering the near-basal position of these wet habitat-adapted lineages and the large number of aquatic lineages in the Araceae sister group (most of the 13 other Alismatales families), an origin of aroids in water-associated swampy habitats is plausible. Second, Late Cretaceous and Palaeocene fossils of free-floating Araceae (*Limnobiophyllum scutatum* and *Cobbania corrugata*; Stockey *et al.*, 1997, 2007; Hoffman & Stockey, 1999) indicate that transitions from a terrestrial growth habit to an aquatic one had occurred early during the evolution of the family. Such transitions are known from other monocots (Cook, 1999) and, even within Araceae, a free-floating habit evolved a third time in the ancestor of the monotypic genus *Pistia*, a member of the derived subfamily Aroideae (Figs 3, S2, node 95, perhaps in the Eocene).

That Laurasia was a region of early Araceae evolution receives support from fossils from the late Aptian to early Albian Figueira da Foz Formation in Portugal (Friis *et al.*, 2010). A newly discovered orontioid leaf fossil from the late Aptian Crato Formation in Brazil indicates that Araceae at that time were also in West Gondwana (C. Coiffard and B. Mohr, Natural History Museum, Berlin, Germany; seen by us in May 2011; Table S2). Until *c.* 65 Ma, the southern tip of West Gondwana/South America provided the only overland connection between West and East Gondwana (Reguero *et al.*, 2002: Fig. 3; Iglesias *et al.*, 2011: Fig. 1d), and Antarctica therefore could have been the route by which the gymnostachyoid clade reached Australia, where it today has a single surviving species. Our AAR, however, does not capture this, probably because of the lack of living or extinct Araceae from Antarctica.

Biogeographically, the presence of orontioid/gymnostachyoid Araceae in the Cretaceous of Brazil and in today's Australia resembles the history of another ancient family, the Calycanthaceae in the Laurales. Members of Calycanthaceae are first known from *c.* 115-Ma-old Crato Formation fossils resembling *Calycanthus* (today three species in North America and China), but also the monotypic Australian genus *Idiospermum* (Mohr & Eklund, 2003). The split between the Northern Hemisphere Calycanthaceae (nine living species) and the Australian *Idiospermum* has been dated to the Late Cretaceous, and a trans-Antarctic overland connection between South America and Australia has been invoked (Zhou *et al.*, 2006). The orontioid Araceae, moreover, resemble Calycanthaceae in exhibiting Miocene Beringian disjunctions, in their case involving the North American/Chinese genera *Calycanthus* and *Chimonanthus* (Zhou *et al.*, 2006) and, in the case of the Araceae, the North American/Asian genera *Symplocarpus* and *Lysichiton* (Nie *et al.*, 2006; our Fig. 3, node 5).

High substitution rates in aquatic Araceae

Seven of the 10 highest DNA substitution rates in the Araceae occur in the free-floating or submerged Lemnoideae, *Pistia* and Cryptocoryneae (Fig. S1, nodes 2, 6, 7 and 10). The literature on molecular substitution rate variation is vast, and there is evidence that rates in both animals and plants can vary with body size, population dynamics, lifestyle and geographical location (Lynch, 2007; Bromham, 2009). Because of this plethora of causes, it is not currently possible to decide whether it is the small body size of aquatic aroids, their mostly clonal reproduction (Lemon *et al.*, 2001) or another feature of their lifestyle that affects the DNA repair efficiency (and hence rates of nucleotide change), or whether it is stressors in their environment that cause particularly high mutation rates.

Extinction in the Northern Hemisphere correlated with climate cooling

Modelling work on the shapes of phylogenetic trees has shown that a long stem leading to a cluster of short branches can indicate a mass extinction (Harvey & Rambaut, 2004; Crisp & Cook, 2009). In the Araceae, the longest branch is that leading from the stem lineage of Lasioideae (Fig. 3, node 28: 90 Ma) to the crown group (node 29: 26 Ma). Lasioid fossils are known from the Late Cretaceous of Siberia and the Eocene of Canada (Smith & Stockey, 2003; Hofmann & Zetter, 2010), but, today, members of Lasioideae survive only in tropical South America, South-East Asia and Africa. The subfamily was thus once more widespread and probably experienced extinction in the Northern Hemisphere when the climate deteriorated at the end of the Oligocene.

Extinction in Eurasia and North America and survival in tropical South-East Asia, South America or Africa indeed seems to be the prevailing pattern in Araceae. Similar effects of Oligocene climate cooling and the Quaternary ice ages have been documented for many plant groups (e.g. Latham & Ricklefs, 1993; Tiffney & Manchester, 2001) which, today, are restricted to tropical America and/or Africa, but in the early Tertiary occurred in Europe, including Anacardiaceae (*Anacardium*), cycads (*Ceratozamia*) and Malphigiaceae (*Tetrapteris*; Manchester *et al.*, 2007). Which of these groups spread across the North Atlantic land bridge, linking North America and Europe by way of Greenland, and which via Beringia, requires case-by-case analyses, and, for the Araceae, remains an open question.

In summary, all eight subfamilies of Araceae formed before the K/T boundary, supporting the view that this extinction event, which was so important for large-bodied animals, had a minor impact on plants, with no major plant groups disappearing at the boundary and the damage primarily confined to the species level (Nichols & Johnson, 2008). Of the 3790 species of Aracaeae described so far, 18 occur in Australia, 17 in Madagascar and 129 in Africa, whereas 1525 are known from the Neotropics and the remainder from tropical Asia and the Malesian archipelago (> 1000 species in some 40 genera; Boyce & Croat, 2011). Yet, the few species in Australia, North America and Eurasia represent more ancient surviving lineages than does the entire tropical Asian region (Fig. 3).

Including past continental plate positions and extinct ranges in biogeographical models

The biogeographical approach used here combines advances made over the past 3 yr (Table 1). Specifically, we modelled changing migration pathways (using different time-slice models) and included ranges that are no longer occupied by adding fossils to the tree file. Any biogeographical model can only 'reconstruct' (infer) areas that are included in the analysis. For example, migration across Eocene Antarctica can only be inferred when Antarctica is included as an operational geographical unit and its connectivity to South America, Australia and India is part of the probability matrix. Thus, one would ideally include all known geographical ranges for a clade by incorporating the location of all of its (well-studied) fossils directly into the analysis. Such formal (quantitative, with measures of uncertainty) AAR goes beyond what can be learned from the fossil record *per se* because it links fossils and their locations with the distribution of living clades in a researcher-driven model.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Inferred DNA substitution rates in the Araceae.

Fig. S2 Results from divergence dating and ancestral area reconstruction (AAR) without fossils.

Fig. S3 Posterior distribution of fossil constraints from the BEAST runs with the simple substitution model (JC + Γ) with either uniform (left column) or gamma-shaped (right column) prior distributions.

Table S1 List of species used in this study with author names, herbarium vouchers and GenBank accession numbers for all sequences

Table S2 Fossils (sorted by age) used as constraints in this study or discussed in the main text

Table S3 Dispersal matrices employed for the maximum likelihood ancestral area reconstructions used in the four-time-slice model (90–60, 60–30), the three-time-slice model (90–30) or both (150–90, 30–0).

Table S4 Divergence age estimates under different molecular clock models in TreeTime, and prior constraint schemes (uniform or gamma) and substitution models (simple, JC + Γ; complex, TPM1uf + Γ for the noncoding region and GTR + Γ for the coding region taking into account the third codon position) in BEAST

Table S5 Results for each node shown in Fig. 3

Table S1. List of species used in this study with author names, herbarium vouchers, and GenBank accession numbers for all sequences. The list is divided into four parts, corresponding to the datasets of (a) Cabrera *et al.*, (2008), (b) additional taxa from Cusimano *et al.*, (2011), (c) additional taxa of this study, and (d) accessions removed from earlier matrices.

a) Accessions from Cabrera *et al.*, (2008).

Species name	Voucher (Herbarium)	Source	*trnL*	*trnL-F*	*trnK/matK*	*rbcL*
Aglaodorum griffithii (Schott) Schott	J. Bogner 1767 (M)	Cabrera *et al.*, 2008	AM932318	AM933314	AM920580	AM905758
Aglaonema modestum Schott ex Engl.	M. Chase 10671 (K)	Cabrera *et al.*, 2008			AM920579	AM905757
Aglaonema modestum Schott ex Engl.	D. Barabé & S.-C. Chantha 86 (MT)	Cabrera *et al.*, 2008	AY054700	AY054700		
Alloschemone occidentalis (Poepp.) Engl. & K.Krause	M. Chase 9996 (K)	Cabrera *et al.*, 2008	AM932310	AM932310	AM920566	AM905744
Ambrosina basii L.	M. Chase 12339 (K)	Cabrera *et al.*, 2008	AM932348	AM932348	AM920620	AM905798
Amorphophallus paeoniifolius (Dennst.) Nicolson	D. Barabé & S.-C. Chantha 98 (MT)	Cabrera *et al.*, 2008	AY054703	AY054703		
Amydrium humile Schott	M. Chase 9974 (K)	Cabrera *et al.*, 2008			AM920567	AM905745
Amydrium zippelianum (Schott) Nicolson	D. Barabé & S.-C. Chantha 99 (MT)	Cabrera *et al.*, 2008	AY054735	AY054735		
Anadendrum sp.	M. Chase 9985 (K)	Cabrera *et al.*, 2008	AM932308	AM932308	AM920547	AM905740
Anaphyllopsis americana (Engl.) A.Hay	M. Chase 11914 (K)	Cabrera *et al.*, 2008			AM920575	AM905753
Anaphyllopsis americana (Engl.) A.Hay	D. Barabé 83 (MT)	Cabrera *et al.*, 2008	AY054726	AY054726		
Anchomanes difformis (Blume) Engl.	M. Chase 10687 (K)	Cabrera *et al.*, 2008			AM920583	AM905761
Anchomanes difformis (Blume) Engl.	D. Barabé 155 (MT)	Cabrera *et al.*, 2008	AY054711	AY054711		
Anthurium acaule (Jacq.) Shott	M. Chase10884 (K)	Cabrera *et al.*, 2008			AM920557	AM905735
Anthurium jenmanii Engl.	D. Barabé & S.-C. Chantha 92 (MT)	Cabrera *et al.*, 2008	AY054730	AY054730		
Anubias barteri Schott	M. Chase 10997 (K)	Cabrera *et al.*, 2008			AM920578	AM905756
Anubias barteri Schott	D. Barabé & S.-C. Chantha 90 (MT)	Cabrera *et al.*, 2008	AY054710	AY054710		
Aridarum nicolsonii Bogner	J. Bogner 2835 (M)	Cabrera *et al.*, 2008	AM932337	AM932337	AM920606	AM905784
Ariopsis peltata J.Grah.	M. Chase 11913 (K)	Cabrera *et al.*, 2008	AM932352	AM932352	AM920626	AM905804
Arisaema franchetianum Engl	M. Chase 10478 (K)	Cabrera *et al.*, 2008	AM932354	AM932354	AM920628	AM905806
Arisarum vulgare O.Targ-Tozz	M. Chase 10992 (K)	Cabrera *et al.*, 2008	AM932347	AM932347	AM920619	AM905797
Arophyton buchetii Bogner	J. Bogner 207 (M)	Cabrera *et al.*, 2008	AM932367	AM932367	AM920642	AM905820
Arum hygrophilum Boiss.	M. Chase 10990 (K)	Cabrera *et al.*, 2008	AM932296	AM932296	AM920631	AM905809

Asterostigma pavonii Schott	M. Sizemore 95-062B (L)	Cabrera *et al.*, 2008	AM932325	AM932325	AM920590	AM905768
Biarum tenuifolium (L.) Schott	M. Chase 282 (K)	Cabrera *et al.*, 2008	AM932357	AM932357	AM920632	AM905810
Bognera recondita (Madison) Mayo & Nicolson	J. Bogner 1995 (M)	Cabrera *et al.*, 2008	AM932322	AM932322	AM920587	AM905765
Bucephalandra motleyana Schott	W. Tomey s.n. (M)	Cabrera *et al.*, 2008	AM932369	AM932369	AM920644	AM905822
Caladium bicolor (Aiton) Vent.	D. Barabé & S.-C. Chantha 96 (MT)	Cabrera *et al.*, 2008	AY054708	AY054708		
Caladium lindenii (André) Madison	M. Chase 10670 (K)	Cabrera *et al.*, 2008			AM920610	AM905788
Calla palustris L.	M. Chase 11802 (K)	Cabrera *et al.*, 2008	AM932366	AM932366	AM920641	AM905819
Callopsis volkensii Engl.	M. Chase 10668 (K)	Cabrera *et al.*, 2008	AM932330	AM932330	AM920595	AM905773
Carlephyton glaucophyllum Bogner	R.D. Mangelsdorff 124 (M)	Cabrera *et al.*, 2008	AM932368	AM932368	AM920643	AM905821
Cercestis mirabilis (N.E.Br.) Bogner	M. Chase 11772 (K)	Cabrera *et al.*, 2008	AM932364	AM932364	AM920639	AM905817
Chlorospatha sp.	M. Chase 11912 (K)	Cabrera *et al.*, 2008	AM932341	AM932341	AM920613	AM905791
Colletogyne perrieri Buchet	O. Pronk s.n. (M)	Cabrera *et al.*, 2008	AM932370	AM932370	AM920645	AM905823
Colocasia esculenta (L.) Schott	M. Chase 10669 (K)	Cabrera *et al.*, 2008	AM932349	AM932349	AM920622	AM905800
Cryptocoryne lingua Becc. ex Engl.	M. Chase 10998 (K)	Cabrera *et al.*, 2008			AM920601	AM905779
Culcasia liberica N.E.Br.	M. Chase 11777 (K)	Cabrera *et al.*, 2008	AM932363	AM932363	AM920638	AM905816
Cyrtosperma macrotum Engl.	M. Chase 11771 (K)	Cabrera *et al.*, 2008	AM932313	AM932313	AM920572	AM905750
Dieffenbachia aglaonemifolia Engl.	M. Chase 10678 (K)	Cabrera *et al.*, 2008			AM920586	AM905764
Dieffenbachia pittieri Engl. & K.Krause	D. Barabé & S.-C. Chantha 88 (MT)	Cabrera *et al.*, 2008	AY054714	AY054714		
Dracontium polyphyllum L.	M. Chase 10688 (K)	Cabrera *et al.*, 2008			AM920569	AM905747
Dracontium polyphyllum L.	D. Barabé 50 (MT)	Cabrera *et al.*, 2008	AY054727	AY054727		
Dracontioides desciscens Engl.	M. Chase 11916 (K)	Cabrera *et al.*, 2008	AM932316	AM932316	AM920576	AM905754
Dracunulus vulgaris Schott	M. Chase 11760 (K)	Cabrera *et al.*, 2008	AM932359	AM932359	AM920634	AM905812
Epipremnum falcifolium Engl.	D. Barabé & Turcotte 100 (MT)	Cabrera *et al.*, 2008	AY054732	AY054732		
Epipremnum pinnatum (L.) Engl.	M. Chase 9977 (K)	Cabrera *et al.*, 2008			AM920568	AM905746
Eminium spiculatum (Blume) Kuntze	M. Chase 11806 (K)	Cabrera *et al.*, 2008	AM932360	AM932360	AM920635	AM905813
Filarum manserichense Nicolson	M. Sizemore 1996-001 (L)	Cabrera *et al.*, 2008	AM932345	AM932345	AM920617	AM905795
Gearum brasiliense N.E.Br.	M. Chase 10693 (K)	Cabrera *et al.*, 2008	AM932321	AM932321	AM920585	AM905763
Gonatopus angustus N.E.Br.	M. Chase 10675 (K)	Cabrera *et al.*, 2008	AM932333	AM932333	AM920599	AM905777
Gorgonidium sp.	Cultivated (L)	Cabrera *et al.*, 2008	AM932324	AM932324	AM920589	AM905767
Gymnostachys anceps R.Brown	M. Chase 9473 (K)	Cabrera *et al.*, 2008	AM932297	AM932297	AM920548	AM905727

Hapaline benthamiana Schott	M. Chase 10676 (K)	Cabrera *et al.*, 2008	AM932339	AM932339	AM920609	AM905787
Helicodiceros muscivorus (L. f.) Engl.	M. Chase 11759 (K)	Cabrera *et al.*, 2008	AM932358	AM932358	AM920633	AM905811
Heteropsis oblongifolia Kunth	Ramírez 11848 (L)	Cabrera *et al.*, 2008			AM920560	AM905737
Heteropsis sp. Barabé	F. Forest & M. Gibernau 147 (MT)	Cabrera *et al.*, 2008	AY054739	AY054739		
Homalomena magna A. Hay	M. Chase 10691 (K)	Cabrera *et al.*, 2008			AM920596	AM905774
Homalomena sp.	D. Barabé 151 (MT)	Cabrera *et al.*, 2008	AY054724	AY054724		
Holochlamys beccarii (Engl.) Engl.	M. Chase 10677 (K)	Cabrera *et al.*, 2008	AM932306	AM932306	AM920558	AM905736
Jasarum steyermarkii G.S.Buting	P.E. Berry & L. Brako 5531 (MO)	Cabrera *et al.*, 2008	AM932342	AM932342	AM920614	AM905792
Lagenandra ovata Thwaites	M. Chase 10991 (K)	Cabrera *et al.*, 2008			AM920602	AM905780
Landoltia punctata (G. Mey) Les & D.J.Crawford	E. Landolt 7248 (—)	Cabrera *et al.*, 2008			AY034185 AY034301	AY034223
Landoltia punctata (G. Mey) Les & D.J.Crawford	M. Chase 14451 (K)	Cabrera *et al.*, 2008	AM932301	AM932301		
Lasia spinosa (L.) Thwaites	M. Chase 11779 (K)	Cabrera *et al.*, 2008	AM932312	AM932312	AM920571	AM905749
Lasimorpha senegalensis Schott	J. Bogner 691 (M)	Cabrera *et al.*, 2008	AM932317	AM932317	AM920577	AM905755
Lemna minor L.	M. Chase 11761 (K)	Cabrera *et al.*, 2008	AM932299	AM932299	AM920552	AM905730
Lysichiton americanus Hultén & H.St.John	M. Chase 11748 (K)	Cabrera *et al.*, 2008			AM920549	AM905728
Lysichiton camtschatcense (L.) Schott	D. Barabé 153 (MT)	Cabrera *et al.*, 2008	AY054740	AY054740		
Mangonia tweediana Schott	J. Bogner 2376 (L)	Cabrera *et al.*, 2008	AM932323	AM932323	AM920588	AM905766
Monstera adansonii Schott	M. Chase 9980 (K)	Cabrera *et al.*, 2008			AM920565	AM905743
Monstera adansonii Schott	D. Barabé & S.-C. Chantha 94 (MT)	Cabrera *et al.*, 2008	AY054734	AY054734		
Montrichardia arborescens (L.) Schott	Cultivated(SING)	Cabrera *et al.*, 2008	AM932365	AM932365	AM920640	AM905818
Nephthytis afzellii Schott	M. Chase10689 (K)	Cabrera *et al.*, 2008			AM920581	AM905759
Nephthytis afzellii Schott	D. Barabé & S.-C. Chantha 95 (MT)	Cabrera *et al.*, 2008	AY054702	AY054702		
Orontium aquaticum L.	Y. Qui 97112 (NCU)	Cabrera *et al.*, 2008	AM932298	AM932298	AM920550	AM905729
Pedicellarum paiei M.Hotta	J. Bogner 2196 (M)	Cabrera *et al.*, 2008	AM932304	AM932304	AM920555	AM905733
Peltandra virginica (L.) Raf.	M. Chase 11770 (K)	Cabrera *et al.*, 2008	AM932362	AM932362	AM920637	AM905815
Philodendron deltoideum Poepp. & Endl.	M. Chase 10891 (K)	Cabrera *et al.*, 2008	AM932331	AM932331	AM920597	AM905775
Phymatarum borneense M.Hotta	M. Chase 10979 (K)	Cabrera *et al.*, 2008	AM932336	AM932336	AM920605	AM905783
Pinellia pedatisecta Schott	M. Chase 11752 (K)	Cabrera *et al.*, 2008	AM932355	AM932355	AM920629	AM905807
Piptospatha ridleyi N.E.Br.	M. Chase 10680 (K)	Cabrera *et al.*, 2008	AM932334	AM932334	AM920603	AM905781
Pistia stratiotes L.	M. Chase 10996 (K)	Cabrera *et al.*, 2008			AM920621	AM905799

Pistia stratiotes L.	D. Barabé 153 (MT)	Cabrera *et al.*, 2008	AY054706	AY054706		
Podolasia stipitata N.E.Br.	M. Chase 11915 (K)	Cabrera *et al.*, 2008	AM932315	AM932315	AM920574	AM905752
Pothoidium lobbianum Schott	J. Bogner 1272 (M)	Cabrera *et al.*, 2008	AM932305	AM932305	AM920556	AM905734
Pothos scandens D.Don	M. Chase 9989 (K)	Cabrera *et al.*, 2008			AM920554	AM905732
Pothos scandens D.Don	D. Barabé & Lavoie 157	Cabrera *et al.*, 2008	AY054731	AY054731		
Protarum sechellarum Engl.	J. Bogner s.n. (M)	Cabrera *et al.*, 2008	AM932353	AM932353	AM920627	AM905805
Pseudodracontium lacourii Schott ex Engl. (Linden & Andre) N.E.Br.	M. Chase 10681 (K)	Cabrera *et al.*, 2008	AM932338	AM932338	AM920608	AM905786
Pseudohydrosme gabunensis Engl.	J.J. Wieringa 3308 (L)	Cabrera *et al.*, 2008	AM932319	AM932319	AM920582	AM905760
Pycnospatha arietina Thorel ex Gagnep.	M. Sizemore s n. (L)	Cabrera *et al.*, 2008	AM932314	AM932314	AM920573	AM905751
Rhaphidophora crassifolia Aldewer.	M. Chase 7398 (K)	Cabrera *et al.*, 2008			AM920563	AM905741
Remusatia vivipara (Roxb.) Schott	M. Chase 11775 (K)	Cabrera *et al.*, 2008	AM932351	AM932351	AM920625	AM905803
Rhodospatha oblongata Poepp. & Endl.	T. Croat 53888 (MO)	Cabrera *et al.*, 2008	AM932307	AM932307	AM920562	AM905739
Scaphispatha gracilis Brongn. ex Schott	E.G. Gonçalves 172 (MO)	Cabrera *et al.*, 2008	AM932343	AM932343	AM920615	AM905793
Schismatoglottis trifasciata Engl.	M. Chase 10692 (K)	Cabrera *et al.*, 2008	AM932335	AM932335	AM920604	AM905782
Scindapsus heredaceus Schott	M. Chase 9986 (K)	Cabrera *et al.*, 2008	AM932309	AM932309	AM920564	AM905742
Spathantheum intermedium Bogner	M. Chase 11776 (K)	Cabrera *et al.*, 2008	AM932326	AM932326	AM920591	AM905769
Spathicarpa hastifolia Hook.	M. Chase 10995 (K)	Cabrera *et al.*, 2008	AM932329	AM932329	AM920594	AM905772
Spathiphyllum wallisii Hort.	M. Chase 210 (NCU)	Cabrera *et al.*, 2008			AM920559	AJ235807
Spathiphyllum wallisii Hort.	D. Barabé & Turcotte 105 (MT)	Cabrera *et al.*, 2008	AY054738	AY054738		
Spathiphyllum wallisii Hort.	S. Mathews 400 (GH)	Cabrera *et al.*, 2008				
Spirodela polyrhiza (L.) Schleid.	M. Chase 11096 (K)	Cabrera *et al.*, 2008	AM932300	AM932300	AM920553	AM905731
Stenospermation popayanense Schott	D. Barabé & Lavoie 159 (MT)	Cabrera *et al.*, 2008	AY054737	AY054737		
Stenospermation ulei K.Krause	M. Chase 9987 (K)	Cabrera *et al.*, 2008			AM920561	AM905738
Steudnera colocasiifolia K.Koch	M. Chase 10682 (K)	Cabrera *et al.*, 2008	AM932350	AM932350	AM920623	AM905801
Stylochaeton bogneri Mayo	M. Chase 10685 (K)	Cabrera *et al.*, 2008	AM932332	AM932332	AM920598	AM905776
Symplocarpus foetidus(L.) Nuttall	J.C. French 219 (CHRB)	Cabrera *et al.*, 2008				L10247
Symplocarpus foetidus (L.) Nuttall	M. Chase 11749 (K)	Cabrera *et al.*, 2008			AM920551	
Symplocarpus foetidus (L.) Nuttall	D. Barabé 154 (MT)	Cabrera *et al.*, 2008	AY054741	AY054741		
Synandrospadix vermitoxicus (Griseb.) Engl.	M. Chase 11774 (K)	Cabrera *et al.*, 2008	AM932328	AM932328	AM920593	AM905771
Syngonium auritum (L.) Schott	M. Chase 10994 (K)	Cabrera *et al.*, 2008	AM932340	AM932340	AM920611	AM905789
Taccarum weddelianum Brongn. ex Schott	E. Hennipman 8315 (L)	Cabrera *et al.*, 2008	AM932327	AM932327	AM920592	AM905770
Typhonium blumei Nicolson & Sivad.	M. Chase 10694 (K)	Cabrera *et al.*, 2008			AM920630	AM905808
Typhonodorum lindleyanum Schott	M. Chase 11780 (K)	Cabrera *et al.*, 2008	AM932361	AM932361	AM920636	AM905814

Ulearum sagittatum Engl.	M. Chase 10695 (K)	Cabrera *et al.*, 2008	AM932344	AM932344	AM920616	AM905794
Urospatha saggitifolia (Rudge) Schott	M. Chase 11773 (K)	Cabrera *et al.*, 2008	AM932311	AM932311	AM920570	AM905748
Wolffia columbiana H.Karts	E. Landolt 7467 (—)	Cabrera *et al.*, 2008			AY034217 AY034333	AY034255
Wolffia columbiana H.Karts	M. Chase 14447 (K)	Cabrera *et al.*, 2008	AM932303	AM932303		
Wolffiella oblonga Hegelm.	E. Landolt 8984 (—)	Cabrera *et al.*, 2008			AY034204 AY034320	AY034242
Wolffiella oblonga Hegelm.	M. Chase 14359 (K)	Cabrera *et al.*, 2008	AM932302	AM932302		
Xanthosoma helleborifolium (Jacq.) Schott	M. Chase 10683 (K)	Cabrera *et al.*, 2008			AM920612	AM905790
Xanthosoma sp.	D. Barabé & Turcotte 107 (MT)	Cabrera *et al.*, 2008	AY054709	AY054709		
Zamioculcas zamiifolia (Lodd.) Engl.	M. Chase 10686 (K)	Cabrera *et al.*, 2008			AM920600	AM905778
Zamioculcas zamiifolia (Lodd.) Engl.	D. Barabé & S.-C. Chantha 84 (MT)	Cabrera *et al.*, 2008	AY054725	AY054725		
Zantedeschia albomaculata (Hook. f.) Bail	M. Chase 11758 (K)	Cabrera *et al.*, 2008	AM932320	AM932320	AM920584	AM905762
Zomicarpella amazonica Bogner	J. Bogner 1985 (M)	Cabrera *et al.*, 2008	AM932346	AM932346	AM920618	AM905796
Acorus calamus L.	J.C.French 232 (CHRB)	Cabrera *et al.*, 2008				M91625
Acorus calamus L.	M.N. Tamura & J. Yamshita 6008 (Bot. Gard. Osaka City Univ.)	Cabrera *et al.*, 2008			AB040154	
Acorus calamus L.	C.A. Joly 226 (MT)	Cabrera *et al.*, 2008	AY054741	AY054741		
Tofieldia pusilla Pers.	C. Lundqvist 12935 (UPS)	Cabrera *et al.*, 2008				AJ286562
Tofieldia pusilla Pers.	M. Chase 1851 (K)	Cabrera *et al.*, 2008	AM932374	AM933370	AM920648	

b) Additional species from Cusimano *et al.*, 2011.

Species name	Voucher (Herbarium)	Source	*trnL*	*trnL-F*	*matK/trnK*	*rbcL*
Anaphyllum wightii Schott	J. Bogner 1833 (M)	Cusimano *et al.*, 2011			HQ687766	
Asterostigma cubense (A. Rich.) K. Krause ex Bogner	E.G. Gonçalves 446 (UB)	Gonçalves *et al.*, 2007	EF173566		EF173531	
Bakoa lucens (Bogner) P.C. Boyce & S.Y. Wong	P.C. Boyce & S.Y. Wong Ar2097 (SAR)	Wong *et al.*, 2010		GQ220962	GQ220894	
Calla palustris L.	J. Bogner 2117 (M)	Cusimano *et al.*, 2011			HQ687765	

Croatiella integrifolia (Madison) E.G. Gonç.	T. Croat 86435 (MO)	Gonçalves *et al.*, 2007	EF173573		EF173538	
Furtadoa sumatrensis M. Hotta	M.Hotta s.n. (M)	Cusimano *et al.*, 2011			HQ687767	
Incarum pavonii (Schott) E.G.Gonç.	W. Hetterscheid H.AR.136 (L)	Gonçalves *et al.*, 2007			EF173548	
Philonotion americanum (A.M.E.Jonker & Jonker) S.Y.Wong & P.C.Boyce	J. Bogner 2911	Wong *et al.*, 2010		GQ220978	GQ220908	
Schottariella mirifica P.C.Boyce & S.Y.Wong	P.C. Boyce *et al.*, Ar1615 (SAR)	Wong *et al.*, 2010		GQ221009	GQ220912	
Theriophonum dalzellii Schott	J. Murata s.n., 21 Aug. 2002	Cusimano *et al.*, 2010; Renner & Zhang, 2004	AY249011	AY248973	EU886534	
Typhonium brownii Schott (to be recombined into the Australian genus *Lazarum* A.Hay)	W. Hetterscheid H.AR.043 (L, spirit coll.)	Cusimano *et al.*, 2010			EU886538	
Sauromatum hirsutum (S.Y.Hu) Cusimano & Hett.	W. Hetterscheid H.AR 036	Renner & Zhang, 2004	AY249014	AY248976		
Sauromatum horsfieldii Miq.	M. Sizemore 96-808	Mansion *et al.*, 2008			EU193593	EU193202
Zomicarpa steigeriana Ferd.Maxim. ex Schott		Batista *et al.*, DS			EU542592	

c) Species newly sequenced for this study.

Species name	Voucher (Herbarium)	Source	*trnL*	*trnL-F*	*matK* /*trnK*	*rbcL*
Alocasia hypnosa J.T.Yin, Y.H.Wang & Z.F.Xu	D. Prehsler 175 (WU)	Nauheimer *et al.*, 2011	JQ238662	JQ238746	JQ238831	
Alocasia odora (Lindl.) K. Koch	P.C. Boyce s.n. (QSBG)	Nauheimer *et al.*, 2011	JQ238679	JQ238764	JQ238848	
Amorphophallus angolensis (Schott) N.E.Br.	HAM 015 (L)	Grob *et al.*, 2002	AF387458		AF387404	AF497061
Amorphophallus paeoniifolius (Dennst.) Nicolson	HAM 378 (L)	Grob *et al.*, 2002			AF387410	AF497091
Apoballis acuminatissima (Schott) S.Y Wong & P.C. Boyce	J. Bogner Ar1197 (SAR)/Bogner 2913 (M)	Wong *et al.*, 2010		GQ220977	GQ220907	
Arisaema amurense Maxim.	J. Bogner, 18 Jul. 2001, BG Munich	Renner & Zhang, 2004	AY248986	AY248948		

Arisaema amurense Maxim.	USSK 176 C-1295 (C)	Petersen *et al.*, 2006				DQ859161
Arisaema costatum (Wall.) Mart.	W. Hetterscheid H.AR. 287	Renner *et al.*, 2004	AY279121	AY275603		
Arisaema dracontium (L.) Schott	T. Barkman 352 (WMU)	Renner & Zhang, 2004	AY248989	AY248951		
Arisaema heterophyllum Blume	G. Gusman 92100	Renner & Zhang, 2004	AY248991	AY248953		
Arisaema heterophyllum Blume	PS3010MT01 (IMD)	Chen *et al.*, 2010				GQ436775
Arisaema macrospathum Benth.	G. Gusman 97229	Renner & Zhang, 2004	AY248992	AY248954		
Arisaema schimperianum Schott	J. Murata s.n.	Renner *et al.*, 2004	AY279133	AY275605		
Arisaema speciosum (Wall.) Mart.	ZH acc. 20041762 (Zurich Botanical Garden)	Mansion *et al.*, 2008	EU193411			EU193196
Arisaema speciosum (Wall.) Mart.	W. Hetterscheid H.AR.294 (L, spirit coll.)	Renner *et al.*, 2004; Cusimano *et al.*, 2010		AY275609	EU886502	
Arisaema tortuosum (Wall.) Schott	W. Hetterscheid 27 Jul 2002 / Anaimudi 20/5	Renner & Zhang, 2004; Cusimano *et al.*, 2010	AY248995	AY248957	EU886577	
Arisaema tortuosum (Wall.) Schott	Leiden cult. 940576	Grob *et al.*, 2002				AF497109
Arisaema triphyllum (L.) Schott	T. Barkman 351 (WMU)	Renner & Zhang, 2004	AY248996	AY248958		AY298817
Arisaema triphyllum (L.) Schott	N. Uhl 93-03 (BH)	Davis *et al.*, 2004				AY298817
Hestia longifolia (Ridl.) S.Y Wong & P.C. Boyce	P.C. Boyce *et al.*, Ar2286 (SAR)	Wong *et al.*, 2010		GQ220996	GQ220928	
Homalomena speariae Bogner & M.D. Moffler	E. Spear s.n. (type) (M)	this paper				
Colocasia gigantea Schott	J. Bogner 427 (M)	Nauheimer *et al.*, 2011	JQ238721	JQ238807	JQ238893	
Colocasia gigantea Schott	ZH acc. 19963234 (Zurich Botanical Garden)	Mansion *et al.*, 2008				EU193194

Nephthytis bintuluensis A. Hay, Bogner & P.B. Boyce	P.C. Boyce AR640 (SAR)	this paper				
Ooia grabowskii (Engl.) S.Y Wong & P.C. Boyce	P.C. Boyce *et al.*, Ar390 (SAR)	Wong *et al.*, 2010		GQ220974	GQ220904	
Pichinia disticha S.Y Wong & P.C. Boyce	P.C. Boyce *et al.*, Ar1761 (SAR)	Wong *et al.*, 2010		GQ220986	GQ220917	
Pistia stratioites L.	J. Bogner BG Munich	this paper				
Protarum sechellarum Engl.	J. Bogner 2992 (M)	Nauheimer *et al.*, 2011	JQ238724	JQ238810		
Remusatia vivipara (Roxb.) Schott	J. Bogner 2982 (M)	Nauheimer *et al.*, 2011	JQ238726	JQ238812	JQ238897	
Rhaphidophora bogneri P.C. Boyce, ined.	J. Bogner 708 (M)	this paper				
Rhaphidophora crassifolia Aldewer.	P.C. Boyce 1226	Tam *et al.*, 2008	AY398511	AY398511		
Steudnera kerrii Gagnep.	J. Bogner 1891 (M)	Cusimano *et al.*, 2008; Nauheimer *et al.*, 2011	EF517218	EF517213	JQ238899	
Typhonium blumei Nicolson & Sivad.	P. Schmidt s.n. (MO)	Renner *et al.*, 2004		AY275630		

d) Accessions removed from earlier matrices to reduce noise in the data set.

Species name	Voucher (Herbarium)	Source	*trnL*	*trnL-F*	matK/trnK	*rbcL*
Alocasia odora (Roxb.) K.Koch.	M. Chase 10674 (K)	Cabrera *et al.*, 2008			AM920624	AM905802
Alocasia odora (Roxb.) K.Koch.	D. Barabé & S.-C. Chantha 93 (MT)	Cabrera *et al.*, 2008	AY054705	AY054705		
Amorphophallus hottae Bogner & Hett.	H.J. Lam s.n. (L)	Cabrera *et al.*, 2008			AM920607	AM905785
Rhaphidophora africana N.E.Br.	D. Barabé & Turcotte 110 (MT)	Cabrera *et al.*, 2008	AY054736	AY054736		
Typhonium giganteum Engl. = *Sauromatum giganteum* (Engl.) Cusimano & Hett.	M. Chase 11803 (K)	Cabrera *et al.*, 2008	AM932356	AM932356		

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Table S2. Fossils (sorted by age) used as constraints in this study or discussed in the main text.

Taxon	Type of fossil	Affinity as stated in original paper; our notes	Location	Geological stratum; Age	Divergence dating: Node; Age	Biogeographic analysis: Node; Area, Age	Reference
Monocots	Pollen	*Liliacidites*, earliest monocot pollen (125 Ma): "The two unequivocal synapomorphies linking *Liliacidites* with monocots as a whole are boat-shaped pollen (33) and liliaceous grading of the reticulum (39)." (Doyle *et al.*, 2008: 66) Estimated ages for Monocot crown: Smith *et al.*, 2010: 156 Ma (**139**–167 Ma) with eudicot calibration. Bell *et al.*, 2010: 130 Ma (123–**138** Ma) with exponential prior.	Trent's Reach, Virginia, Potomac Group, USA	Early Aptian 125 Ma or somewhat younger	Node #0 (root); 125–139 Ma (normal distribution: mean 132, stdev. 4.25)		Doyle, 1992; Doyle *et al.*, 2008; Bell *et al.*, 2010; Smith *et al.*, 2010
Mayoa portugallica	Pollen	Araceae, possibly Monsteroideae; The exine structure is "rarely columellae-like" (Friis *et al.*, 2004: 16566), raising the possibility that the grain might be from a gymnosperm	Torres Vedras, Figueira da Foz Formation, Portugal	Aptian – early Albian 125 or 112 Ma			Friis *et al.*, 2004, 2006, 2010; Heimhofer *et al.*, 2007;
Unpublished aroid, Crato Formation	Leaf	Basal Araceae, possibly Orontioideae (personal communication from J. Bogner, B. Mohr, and C. Coiffard, 30 May 2011)	Crato Formation, Brazil	Late Aptian, 115 Ma			C. Coiffard & B. Mohr, 1 Sep 2011
Araceae fossil A	Inflorescence fragments, *in situ* pollen	"All characters of the new fossil strongly support a close relationship with the true aroids, subfamily Aroideae, which are characterized by their unisexual, perianth-less flowers (Cabrera *et al.*, 2008)." (p. 376)	Vila Verde, Figueira da Foz Formation, Portugal	Late Aptian to early Albian 112 Ma			Friis *et al.*, 2010
Araceae fossil B	Inflorescence with flowers, *in situ* pollen	Araceae; "The characters of this fossil indicate a phylogenetic relationship to subfamily Pothoideae." (p. 376)	Vila Verde, Figueira da Foz Formation, Portugal	Late Aptian – early Albian 112 Ma			Friis *et al.*, 2010
Albertarum pueri	Infructescence	"The fossil is referred to the subfamily Orontioideae" (p. 593)	Horseshoe Canyon Formation, Southern Alberta, Cananda	Late Campanian 72 Ma	Node #3; 72 Ma	Node #f1; North America; 72 Ma	Bogner *et al.*, 2005

Lysichiton austriacus	Leaf	"This species is undoubtedly another Late Cretaceous representative of the subfamily Orontioideae. The venation pattern is a good match for that of *Lysichiton* (Figs 19–20) in having simple pinnate primary lateral veins that are connected with regular quadrangular meshes of transverse reticulate higher-order venation…" (p. 142)	Grünbach, Austria	Lower Campanian 70 Ma		Node #f2; Eurasia; 70 Ma	Bogner *et al.*, 2007
Lasioideaecidites hessei	Pollen	"*Lasioideaecidites hessei* and *Lasioideaecidites bogneri*, represents the earliest record of the subfamily Lasioideae (Araceae)." (p. 170) "The two taxa of the newly described fossil genus *Lasioideaecidites*, i.e. *Lasioideaecidites hessei* (with no comparable extant genus) and *L. bogneri* (resembles the genus *Cyrtosperma*), were affiliated to the primitive subfamily Lasioideae because it is the only angiosperm group that has a characteristic thickening of endexinous/nexine material in the sulcus area on the distal side of the pollen grains (Hesse, 2002, figures 3–4; and Hesse, pers. comm., 2010)" (p. 189)	Tyung River outcrop, centre of the Vilui Basin, Timerdyakh Formation, sample T9, Siberia	Latest Campanian – earliest Maastrichtian 75–70 Ma	Node #28; 70 Ma	Node #f6; Eurasia; 70 Ma	Hofmann & Zetter, 2010
Rhodospathodendron tomlinsonii	Axis	"This fossil has further similarity with *Rhodospatha* in having a central vascular cylinder with compact arrangement of collateral, amphivasal, and compound bundles and a large number of angular metaxylem vessels. The fossil thus matches best with *Rhodospatha*." (p. 90)	Deccan Intertrappean Beds of Nawargaon in Wardha District, Maharashtra, India	Late Maastrichtian – Danian 65.5 Ma			Bonde, 2000
Orontium mackii	Leaf	"While fragmentary, they are clearly relatable to *Orontium*." (p. 138)	McRae Formation, Jose Creek Member, New Mexico, USA	Maastrichtian 70.6–65.5 Ma		Node #f3; North America; 65.5 Ma	Bogner *et al.*, 2007
Symplocarpus hoffmaniae	Leaf	"They most closely resemble the genus *Symplocarpus* (Figs. 25–26)." (p. 140); tribe Orontioideae	Mud Buttes (=Dean Street), Bowman County, North Dakota, USA	Uppermost Maastrichtian 65.5 Ma			Bogner *et al.*, 2007
Cobbania corrugata (Pistia corrugata)	Stems, attached leaves, and roots	"We develop a reconstruction of the plant based on attached organs and compare the fossils with the fossil *Limnobiophyllum* and extant *Pistia*, revealing a greater systematic and ecological diversity of Late Cretaceous Araceae than previously recognized" (p. 609).	Dinosaur Park Formation Alberta, Canada	Campanian 83.5–70.6 Ma			Stockey *et al.*, 2007

Limnobiophyllum scutatum	Sterile plants	Lemnoideae; "Therefore, and because no information on flowers and fruits is available, *Limnobiophyllum* may serve as a tentative link of the Araceae with the Lemnaceae - a model visualized many years ago by Schleiden (1839)." (Kvacek 1995: 59); assignment of *Limnobiophyllum* to Lemnoideae (Bogner 2009: 122)	USA (Maastrichtian to Oligocene), Canada (Paleocene), East Russia (Paleocene)	Maastrichtian to Oligocene	Node #6; 65.5 Ma		Kvacek, 1995; Stockey *et al.*, 1997; Johnson, 2002; Bogner, 2009; Pigg & DeVore, 2010;
Montrichardia aquatica	Leaf	"…the collective venation pattern and higher order veins characterize the extant genus *Montrichardia* and the fossil *M. aquatica*, …" (p. 1580)	Rancheria Basin, Cerrejón Formation, Cerrejón coal mine, Colombia	Mid to Late Paleocene 61.7–55.8 Ma	Node #44; 55.8 Ma	Node #f8; South America; 55.8 Ma	Herrera *et al.*, 2008
Petrocardium cerrejonense	Leaf	"*Petrocardium wayuuorum* and *P. cerrejonense* have similar venation patterns to many modern species of *Anthurium* in terms of collective venation, and secondary and higher order veins types (Table 1)." (p. 1575)	Rancheria Basin, Cerrejón Formation, Cerrejón coal mine, Colombia	Mid to Late Paleocene 61.7–55.8 Ma	Node #13; 55.8 Ma	Node #f4; South America; 55.8 Ma	Herrera *et al.*, 2008
Nitophyllites zaisanicus	Leaf	"…, we prefer to match *N. zaisanicus* with *Typhonodorum* (fig. 9), which shares most of the venation characters, including the ultimate areolation, rather than with *Peltandra* or *Colocasia*." (p. 170), "However, a direct assignment to a particular extant genus is not warranted on the basis of available details of the venation." (p. 170)	Kiin-Kerish Formation, Zaisan Basin, Kazakhstan	Paleocene 65.5–55.8 Ma	Node #62; 55.8 Ma	Node #f9; Eurasia; 55.8 Ma	Iljinskaja, 1986; Wilde *et al.*, 2005
Keratosperma allenbyense	Seeds	"More detailed knowledge of anatomy of *Keratosperma* and other lasioid seeds (Seubert 1993, 1997) reinforces the placement of *Keratosperma* in Araceae, subfamily Lasioideae. Seeds of taxa from this subfamily are characterized as anacampylotropous, having a hard seed coat with crests and warts, starch-free endosperm, and curved embryos (Seubert 1997). In addition, specialized micropylar and chalazal regions are not common among Araceae but are found in most Lasioideae (Seubert 1997). Therefore, it seems that our fossil seeds can be placed with some confidence in this subfamily. " (p. 245–248)	Princeton Chert, British Columbia, Canada	Middle Eocene 48.7 Ma (age given by Smith and Stockey, 2003)		Node #f7; North America; 48.7 Ma	Smith & Stockey, 2003
Caladiosoma messelense	Leaf	"The more complete specimen best matches some members of the Old World tribe Colocasieae (e.g., *Alocasia*) that extend from the tropics into the humid paratropical- subtropical zone in southern China. The New World tribe Caladieae is also indistinguishable on the basis of the leaf morphology, although the	Messel Formation, Germany	Lower Geiseltalian 47.5–47 Ma (email from de Wilde to SR, 7 Jan. 2009)			Wilde *et al.*, 2005

		affinities seem less probable for paleobiogeographic reasons." (p. 167)					
Araciphyllites tertiarius	Leaf	"In the venation patterns and the consistently missing petiole *A. tertiarius* corresponds to tribe Monstereae (Mayo *et al.*, 1997). Similar leaves occur in Old World *Epipremnum* (including partly dissected leaves), *Rhaphidophora*, and *Scindapsus*." (p. 165).	Messel Formation, Germany	Lower Geiseltalian 47.5–47 Ma (Email from de Wilde to SR, 7 Jan. 2009)	Node #20; 47.0 Ma	Node #f5; Eurasia; 47.0 Ma	Wilde *et al.*, 2005
Orontium wolfei	Leaf	"This morphotype matches, in all essential features, the only extant representative of the genus *Orontium*, *O. aquaticum* L., whose venation pattern is unique among aroids…" (p. 136)	Northern Washington, USA; Southern British Columbia, Canada	Lower–middle Eocene 48.6–37.2 Ma			Bogner *et al.*, 2007
Nitophyllites limnestis		"The *Philodendron* leaf reported here is the only fossil record of this genus. Careful comparison of the anatomy and morphology of the fossil leaf to that of numerous extant genera provides a sound and reliable basis upon which to accept this fossil record" Dilcher and Daghlian 1977 (p.531) "As already pointed out for the latter case by Bown (1988, p. 34) and Mayo (1991), such a marginal pattern corresponds with that found in some genera of subfamily Aroideae, namely tribe Peltandreae (*Peltandra*, *Typhonodorum*) and tribe Arophyteae, but not in tribe Philodendreae (*Philodendron*)." Wilde *et al.*, 2005 (p.170)	Claiborne Formation, Henry Co., Tennessee, USA	Middle Eocene 48.6–37.2 Ma			Dilcher & Daghlian 1977 Wilde *et al.*, 2005
Nitophyllites bohemicus	Leaf	"The affinities of *N. bohemicus* to extant genera remain obscure because various representatives of tribes Peltandreae and Arophyteae may develop a similar type of large leaves. The parallel-pinnate venation indicates affinities to *Peltandra*, which differs in more steeply angled and widely spaced crossveins, and to *Typhonodorum* (fig. 9), which often shows perpendicular crossveins." (p.173)	Kuclin, Czech Republic	Lower Eocene 40.4–33.9 Ma			Wilde *et al.*, 2005
Arisaema hesperia	Inflorescence	Electronic discussion at http://www.amjbot.org/letters/	Latah Formation near Spokane, USA	Miocene 18–16 Ma (15.8 Ma, Graham 1999)			Knowlton, 1926; Graham 1999; Renner *et al.*, 2004a,b

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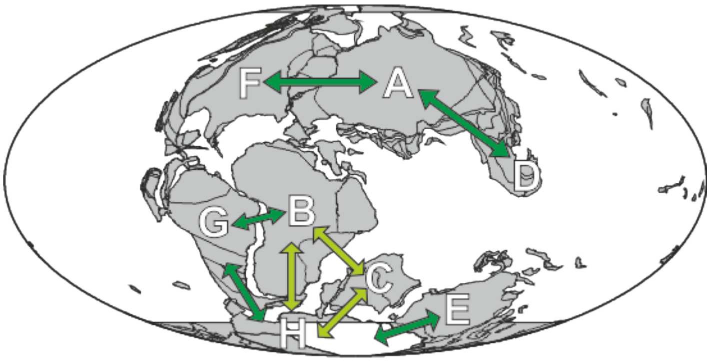
Table S3. Dispersal matrices used for the maximum likelihood ancestral area reconstructions used in the 4-time-slice model (90–60, 60–30), the 3-time-slice model (90–30), or both (150–90, 30–0). Dispersal probabilities are given as $p = 1$ for connected and neighboring areas, $p = 0.5$ for partly connected (meaning for part of the time), $p = 0.01$ for not connected or not neighboring, and $p = 0.1$ for transitions between any area and the widely distributed "water-associated" plants.

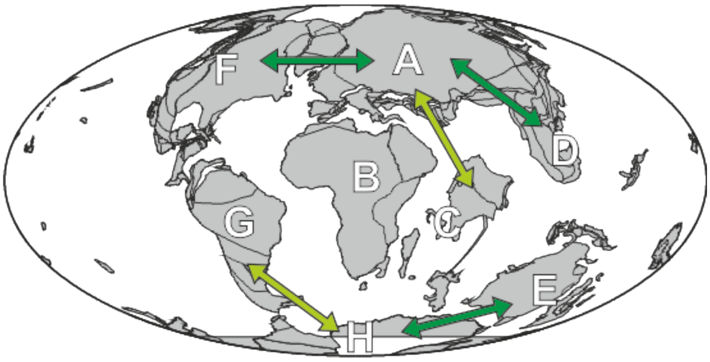
150–90 Ma

	A	B	C	D	E	F	G	H	I
A	1	0.01	0.01	1	0.01	1	0.01	0.01	0.1
B	0.01	1	0.5	0.01	0.01	0.01	1	0.5	0.1
C	0.01	0.5	1	0.01	0.01	0.01	0.01	0.5	0.1
D	1	0.01	0.01	1	0.01	0.01	0.01	0.01	0.1
E	0.01	0.01	0.01	0.01	1	0.01	0.01	1	0.1
F	1	0.01	0.01	0.01	0.01	1	0.01	0.01	0.1
G	0.01	1	0.01	0.01	0.01	0.01	1	1	0.1
H	0.01	0.5	0.5	0.01	1	0.01	1	1	0.1
I	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	1



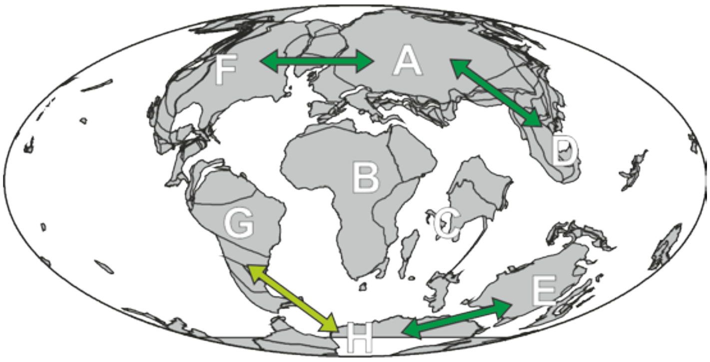
90–30 Ma (used in 3-time-slice model)

	A	B	C	D	E	F	G	H	I
A	1	0.01	0.5	1	0.01	1	0.01	0.01	0.1
B	0.01	1	0.01	0.01	0.01	0.01	0.01	0.01	0.1
C	0.5	0.01	1	0.01	0.01	0.01	0.01	0.01	0.1
D	1	0.01	0.01	1	0.01	0.01	0.01	0.01	0.1
E	0.01	0.01	0.01	0.01	1	0.01	0.01	1	0.1
F	1	0.01	0.01	0.01	0.01	1	0.01	0.01	0.1
G	0.01	0.01	0.01	0.01	0.01	0.01	1	0.5	0.1
H	0.01	0.01	0.01	0.01	1	0.01	0.5	1	0.1
I	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	1



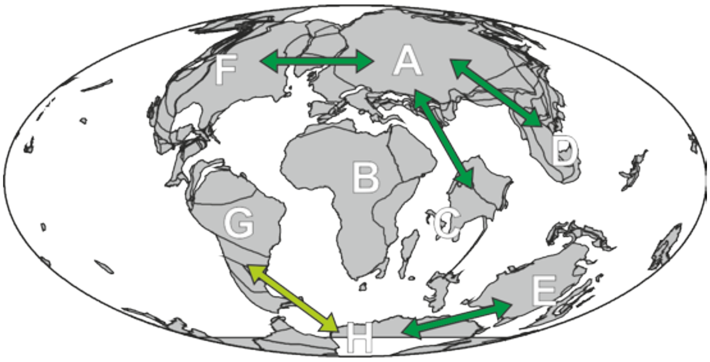
90–60 Ma (used in the 4-time-slice model)

	A	B	C	D	E	F	G	H	I
A	1	0.01	0.01	1	0.01	1	0.01	0.01	0.1
B	0.01	1	0.01	0.01	0.01	0.01	0.01	0.01	0.1
C	0.01	0.01	1	0.01	0.01	0.01	0.01	0.01	0.1
D	1	0.01	0.01	1	0.01	0.01	0.01	0.01	0.1
E	0.01	0.01	0.01	0.01	1	0.01	0.01	1	0.1
F	1	0.01	0.01	0.01	0.01	1	0.01	0.01	0.1
G	0.01	0.01	0.01	0.01	0.01	0.01	1	0.5	0.1
H	0.01	0.01	0.01	0.01	1	0.01	0.5	1	0.1
I	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	1



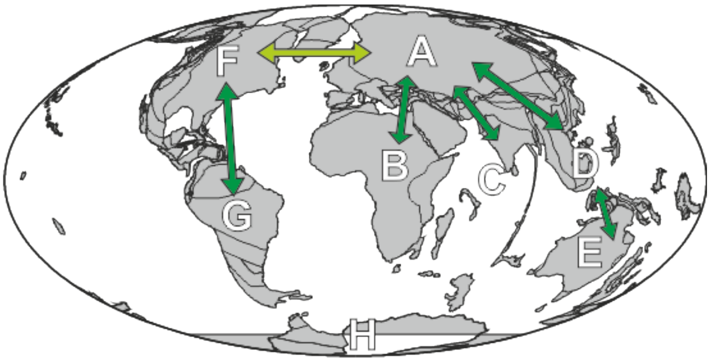
60–30 Ma (used in the 4-time-slice model)

	A	B	C	D	E	F	G	H	I
A	1	0.01	1	1	0.01	1	0.01	0.01	0.1
B	0.01	1	0.01	0.01	0.01	0.01	0.01	0.01	0.1
C	1	0.01	1	0.01	0.01	0.01	0.01	0.01	0.1
D	1	0.01	0.01	1	0.01	0.01	0.01	0.01	0.1
E	0.01	0.01	0.01	0.01	1	0.01	0.01	1	0.1
F	1	0.01	0.01	0.01	0.01	1	0.01	0.01	0.1
G	0.01	0.01	0.01	0.01	0.01	0.01	1	0.5	0.1
H	0.01	0.01	0.01	0.01	1	0.01	0.5	1	0.1
I	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	1



30–0 Ma

	A	B	C	D	E	F	G	H	I
A	1	1	1	1	0.01	0.5	0.01	0.01	0.1
B	1	1	0.01	0.01	0.01	0.01	0.01	0.01	0.1
C	1	0.01	1	0.01	0.01	0.01	0.01	0.01	0.1
D	1	0.01	0.01	1	1	0.01	0.01	0.01	0.1
E	0.01	0.01	0.01	1	1	0.01	0.01	0.01	0.1
F	0.5	0.01	0.01	0.01	0.01	1	1	0.01	0.1
G	0.01	0.01	0.01	0.01	0.01	1	1	0.01	0.1
H	0.01	0.01	0.01	0.01	0.01	0.01	0.01	1	0.1
I	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	1



Graphics were produces using the plate-tectonic reconstruction service of the www.odsn.de website. The reconstructions are based on Hay et al. 1999.

Hay WW, DeConto R, Wold CN, Wilson KM, Voigt S, Schulz M, Wold-Rossby A, Dullo W-C, Ronov AB, Balukhovsky AN, Soeding E. (1999): Alternative global Cretaceous paleogeography. Pp. 1–47 in Barrera E, Johnson C (Eds.), *The Evolution of Cretaceous Ocean/Climate Systems, Geological Society of America Special Paper 332.*

Table S4. Divergence age estimates under different molecular clock models in TreeTime, and prior constraint schemes (uniform or gamma) and substitution models (simple: JC+Γ, complex: TPM1uf+Γ for the non-coding region and GTR+Γ for the coding region taking into account the third codon position) in BEAST. Ages are given only for nodes with high support (posterior probability ≥0.95). Node numbers are the same in all figures and tables.

Node #	Compound poisson process (CPP)	Dirichlet model (DM)	Uncorrelated exponential model (UCED)	Uncorrelated lognormal model (UCLN)	Uncorrelated lognormal model in BEAST uniform prior, simple subst. model	Uncorrelated lognormal model in BEAST uniform prior, complex subst. model	Uncorrelated lognormal model in BEAST gamma prior, simple subst. model	Uncorrelated lognormal model in BEAST with gamma prior, complex subst. model
0	166.29 (132.71–196.99)	185.96 (163.18–217.58)	146.36 (129.54–165.34)	204.44 (179.74–228.59)	137.76 (130.22–145.65)	137.5 (129.19–145.56)	142.73 (127.09–159.79)	143.21 (128.35–160.95)
1	160.94 (133.63–189.65)	182.34 (160.98–217.45)	142.45 (125.47–160.08)	200.27 (177.46–222.53)	135.02 (125.79–143.54)	134.52 (124.05–144.44)	138.35 (121.6–157.23)	139.07 (122.84–156.87)
2	142.07 (120.58–165.47)	159.71 (143.35–186.78)	128.27 (114.62–144.25)	178.03 (157.61–200.86)	121.68 (112.01–131.9)	121.56 (110.64–132.26)	121.82 (106.32–139.11)	122.15 (107.7–138.57)
3	129.87 (110.68–153.59)	109.53 (78.17–137.08)	90.64 (68.19–109.66)	132.74 (96.25–161.63)	95.58 (73.18–115.48)	95.9 (72.86–115.37)	91.3 (71.1–112.02)	91.24 (70.5–111.47)
4	78.67 (51.02–123.49)	66.29 (43.36–92.27)	47.75 (19.82–69.68)	75.56 (41.04–107)	52.81 (28.39–77.24)	52.08 (27.42–77.55)	50.9 (27.53–72.74)	49.05 (26.88–73.34)
5	26.24 (13.23–40.34)	21.98 (9.78–37.79)	20.12 (5.56–34.38)	25.78 (11.13–45.67)	20.6 (6.96–37.74)	20.1 (6.66–36.45)	19.61 (6.94–34.78)	19.1 (6.69–34.19)
6	109.4 (92.3–125.79)	125.69 (108.43–140.89)	106.69 (94.42–117.97)	144.19 (127.67–158.49)	103.55 (93–113.45)	103.97 (92.82–115.1)	101.32 (88.05–115.76)	102.07 (88.7–115.2)
7	50.43 (41.91–61.37)	94.41 (79.7–106.25)	71.7 (59.91–84.63)	106.67 (88.87–131.08)	73.37 (59.46–87.91)	73.98 (56.56–88.57)	70.88 (55.06–85.67)	71.02 (55.57–85.59)
8	31.07 (22.72–39.15)	76.18 (63.26–88.49)	55.29 (45.23–66.67)	83.5 (66.25–102.1)	55.54 (41.4–70.36)	56.81 (40.3–72.03)	54.26 (40.65–68.61)	54.3 (39.92–69.04)
10	12.2 (6.41–19.2)	43.57 (33.65–53.6)	29.63 (20.26–39.05)	43.43 (17.76–63.59)	29.12 (18.33–40.48)	29.39 (17.29–43.66)	28.07 (17.81–40.17)	28.94 (18.34–40.93)
11	103.84 (89.35–118.3)	107.65 (89.12–122.14)	98.38 (85.11–110.73)	130.14 (114.16–147.21)	96.73 (86.62–107.06)	97.43 (85.89–108.47)	93.36 (81.22–106.71)	94.29 (82.77–106.99)
12	90.1 (77.21–105.28)	87.43 (72.56–104.98)	86.54 (72.54–102.18)	104.87 (82.95–124.97)	81.06 (68.3–93.68)	82.25 (67.24–95.82)	78.17 (64.35–92.46)	78.53 (64.75–92.32)
13	72.31 (60.28–85.85)	64.69 (50.87–80.03)	65.01 (51.99–81.2)	76.31 (55.21–100.62)	64.51 (55.8–76.54)	65.38 (55.8–78.83)	61.64 (50.47–74.22)	61.55 (50.21–73.77)
14	27.18 (20.18–35.04)	31.51 (17–48.17)	28.44 (13.15–43.45)	30.8 (14.92–48.14)	26.13 (11.72–41.24)	28.2 (11.55–46.35)	25.77 (11.96–41.5)	25.62 (12.93–41.29)
15	22.04 (15.78–28.65)	22.85 (11.11–34.18)	17.15 (5.89–28.01)	22.16 (10.13–38.78)	18.14 (6.62–31.62)	19.64 (6.35–34.74)	18.2 (6.55–31.01)	18.05 (6.8–31.33)
16	48.89 (42.36–55.26)	54.58 (40.85–72.04)	62.1 (48.51–75.68)	56.76 (44.67–68.24)	54.66 (47.03–63.99)	56.34 (47.14–69.2)	51.78 (42.37–63.11)	51.06 (41.79–61.3)
17	34.81 (27.11–41.17)	33.17 (20.72–48.62)	35.66 (16.66–59.17)	38.88 (23.74–54.64)	31.5 (17.92–47.05)	34.16 (16.11–50.89)	31.48 (17.23–46.53)	30.79 (16.66–44.51)
18	28.32 (20.62–34.53)	24.73 (14.59–38.61)	25.01 (13.36–40.48)	28.69 (16.95–41.34)	22.61 (10.34–36.36)	24.2 (9.61–39.06)	23.22 (10.59–36.16)	21.83 (10.49–34.17)
19	23.36 (15.67–30.6)	17.58 (7.15–26.32)	14.89 (4.46–26.72)	21.61 (7.94–34.94)	16.21 (5.16–28.31)	17.13 (4.9–30.56)	16.65 (5.92–28.69)	15.61 (5.49–27.19)
20	46.3 (41.07–51.86)	51.45 (41.3–68.59)	55.58 (42.94–70.15)	52.7 (42.58–62.25)	51.38 (47–59.35)	52.62 (47–63.11)	48.43 (41.08–58.34)	47.94 (40.91–57.17)
21	29.38 (21.21–38.18)	28.38 (14.81–40.11)	42.44 (23.13–61.22)	32.42 (19.16–43.54)	27.69 (16.29–40.77)	29.75 (14.91–43.83)	26.34 (15.78–39.24)	26.18 (15.8–38.03)
22	26.1 (18.66–34.02)	22.96 (9.85–35.52)	34.1 (13.53–53.67)	27.81 (16.7–39.13)	23.14 (12.16–35.29)	24.75 (11.87–37.97)	22.08 (11.88–33.6)	21.85 (12.05–32.18)
23	22.3 (15.47–29.42)	17.85 (7.71–27.89)	26.74 (10.43–47.87)	22.42 (12.52–34.45)	17.91 (8.34–28.8)	19.21 (8.09–31.29)	17.21 (8.09–27.54)	17.25 (8.83–26.8)
24	14.94 (8.93–20.57)	10.53 (4.06–19.93)	15.87 (3.44–34.41)	13.17 (5.39–23.91)	10.93 (3.72–19.71)	11.82 (3.29–21.31)	10.82 (3.02–18.93)	10.75 (4.14–19.13)
25	24.63 (17.03–34.55)	23.71 (12.74–36.16)	27.5 (10.38–45.07)	26.28 (12.01–37.91)	21.99 (10.74–34.89)	23.37 (10.18–37.59)	21.26 (10.72–34.09)	20.89 (10.7–32.54)
26	15.38 (8.53–22.91)	12.61 (4.24–24.43)	15.99 (2.81–32.74)	13.83 (4.78–24.66)	12.15 (3.34–22.39)	13.16 (3.49–24.47)	11.81 (3.49–21.17)	11.8 (3.74–21.15)
27	20.3 (15.14–26.71)	20.49 (7.38–32.46)	24.92 (5.42–48.74)	23.29 (11.75–36.49)	21.05 (6.7–36.42)	21.56 (6.56–38.2)	16.65 (5.92–28.69)	19.79 (6.28–33.96)

28	94.44 (80.55–108.76)	93.99 (75.65–108.09)	91.69 (80.22–103.43)	116.93 (97.6–134.67)	90.23 (80.09–100.68)	91.38 (78.73–102.33)	85.76 (74.61–97.03)	87.05 (75.86–98.55)
29	24.05 (17.84–30.49)	27.71 (16.05–40.14)	30.45 (11.89–50.15)	32.25 (20.54–42.99)	26.38 (15–37.84)	29.51 (13.45–47.76)	24.7 (14.5–35.9)	24.97 (15.07–36.32)
36	16.26 (11.31–22.02)	15.58 (7.52–24.18)	14.39 (2.54–27.36)	20.49 (11.07–36.38)	16.3 (6.62–26.5)	17.82 (7.08–29.59)	15.76 (7.22–24.65)	15.6 (6.8–25.15)
38	90.35 (76.78–103.88)	89.33 (74.49–100.32)	88.01 (79.11–102.55)	109.58 (90.07–128.76)	86.95 (77.1–97.03)	87.88 (76.61–98.58)	82.22 (72.19–93.09)	83.46 (72.8–94.36)
39	77.36 (62.57–91.31)	70.87 (43.79–93.5)	63.76 (34.27–86.48)	92.74 (56.31–119.35)	66.95 (41.1–86.91)	67.57 (40.21–88.77)	64.08 (40.85–84.27)	65.52 (41.08–85.97)
40	25.46 (18.35–35)	24.46 (8.52–47.64)	33.81 (8.04–60.09)	29.57 (8.12–52.3)	22.73 (5.69–41.84)	23.79 (6.11–43.67)	21.63 (6.76–39.45)	21.77 (6.82–40.24)
41	84.51 (72.7–96.22)	83.1 (72.31–93.86)	82.61 (72.61–97.53)	98.1 (82.74–120.83)	82.12 (73.24–92.28)	80.62 (70.95–89.64)	77.14 (67.44–87.05)	78.24 (68.63–88.69)
47	62.49 (55.81–71.14)	62.08 (54.85–70.63)	61.57 (54.32–71.21)	70.2 (60.79–81.17)	66.18 (60.34–72.84)	67.39 (59.31–75.22)	61.69 (54.9–69.35)	61.47 (55.02–68.9)
48	57.64 (50.4–66.76)	54.23 (44.88–62.48)	53.71 (38.22–65.61)	64.04 (54.47–75.52)	58.49 (47.42–68.23)	60.1 (44.62–71.55)	54.78 (43.09–64.86)	54.81 (44.45–64.1)
49	26.99 (20.44–35.43)	23.61 (13.33–37.67)	27.18 (13.38–47.32)	26.9 (17.11–37.09)	24.17 (9.76–40.43)	25.91 (8.98–42.95)	24.82 (10.93–39.51)	22.68 (10.52–36.93)
51	39.55 (32.34–48.6)	40.38 (32.23–48.74)	37.59 (26.86–50.1)	47.44 (37.34–58.6)	42.02 (30.47–54.14)	44.15 (28.52–58.06)	39.84 (29.15–51.37)	39.88 (29.06–50.74)
52	34.27 (26.9–43.91)	34.98 (20.97–43.94)	26.44 (15.09–42.43)	40.36 (27.1–55.81)	34.24 (18.88–49.35)	35.07 (15.48–50.4)	32.53 (17.89–46.02)	32.62 (18.48–46.91)
53	36.99 (30.03–45.54)	36.78 (29.24–44.75)	32.89 (20.81–46.39)	42.94 (32.8–54.78)	37.62 (26.7–48.81)	39.67 (24.73–52.6)	35.85 (25.42–46.33)	35.91 (25.09–45.85)
54	21.84 (15.23–29.25)	21.98 (10.73–32.39)	18.2 (3.81–38.09)	25.35 (6.75–40.15)	20.28 (7.2–34.13)	21.64 (5.75–36.84)	19.65 (7.5–32.73)	19.54 (7.43–32.24)
55	33.27 (27.39–41.2)	31.51 (25.48–40.01)	27.13 (17.6–36.85)	37.18 (27.97–48.57)	32.08 (22.18–42.91)	33.87 (20.43–46.12)	30.79 (21.42–40.79)	30.71 (21.47–40.63)
56	13.81 (8.97–19.31)	14.26 (5.82–24.13)	12.57 (2.02–24.94)	15.39 (7.28–25.77)	13.64 (4.55–23.39)	15.08 (3.72–26.14)	13.37 (4.36–23.66)	13.06 (4.42–22.62)
58	17.33 (11.14–23.78)	16.86 (8.7–26.02)	14.44 (6.53–24.31)	19.81 (10.86–30.53)	16.74 (7.9–26.57)	17.84 (6.58–27.66)	16.23 (7.07–25.62)	15.95 (7.71–25.17)
59	6.37 (2.21–10.81)	6.27 (1.81–11.24)	6.25 (1.21–13.71)	8.03 (1.78–14.97)	6.49 (1.44–12.65)	7.02 (1.38–13.88)	6.13 (1.47–11.98)	6.16 (1.48–11.96)
60	17.71 (10.07–25.84)	18.46 (10.6–26.26)	14.4 (6.4–22.82)	19.55 (9.49–28.69)	16.87 (7.23–27.34)	18.07 (6.47–29.35)	17.06 (7.65–26.37)	16.29 (7.7–26.43)
61	58.22 (53.03–65.16)	57.69 (52.16–63.99)	57.57 (51.52–65.25)	63.87 (54.54–74.61)	62.25 (57.77–67.78)	63.64 (56.88–70.53)	57.76 (51.72–64.29)	57.53 (52.26–63.76)
62	51.73 (49.36–55.44)	52.3 (49.47–56.66)	53.08 (49.51–58.07)	55.37 (49.58–62.08)	57.46 (55.8–60.67)	58.4 (55.8–62.33)	52.62 (49.42–57.11)	52.42 (49.4–56.51)
63	30.96 (24.82–37.94)	32.68 (19.19–44.53)	26.61 (9.95–44.69)	33.71 (18.8–44.31)	29.57 (12.46–47.42)	30.9 (11.81–48.87)	27.1 (11.08–43.78)	27.7 (12.32–43.83)
64	43.74 (31.32–51.21)	36.52 (20.65–51.78)	43.55 (29.05–53.47)	42.53 (25.27–54.17)	38.85 (20.53–56.28)	39.63 (19.04–57.18)	36.76 (19.06–52.35)	36.35 (19.37–51.26)
65	36.92 (24.97–47.25)	25.02 (12.33–39.57)	35.02 (19.55–48.75)	35.28 (18.67–51.23)	29.27 (13.89–48.71)	30.58 (12.5–49.52)	27.71 (12.62–44.61)	28.23 (13.81–45.03)
66	30.32 (19.62–40.63)	18.81 (9.2–29.53)	21.1 (8.4–36.43)	26.51 (11.26–42.04)	21.27 (7.75–38.52)	22.4 (7.59–39.87)	20.39 (7.35–35.27)	20.78 (7.76–35.47)
67	5.12 (1.4–9.56)	3.29 (0.7–6.8)	4.76 (0.31–16.47)	4.59 (0.75–9.75)	3.68 (0.32–8.34)	4.01 (0.38–9.07)	3.62 (0.39–7.91)	3.46 (0.45–7.79)
68	39.04 (32.66–46.85)	39.73 (31.68–48.24)	42.97 (30.62–53.02)	46.71 (37.39–57.15)	45.68 (35.09–55.26)	48.12 (30.95–62.02)	43.43 (32.21–53.74)	43.04 (33.83–52.45)
69	34.38 (28.32–40.82)	32.72 (26.07–39.95)	33.91 (23.17–43.87)	38.45 (30.38–46.2)	38.97 (30.17–48.2)	36.6 (24.73–46.37)	33.49 (24.89–42.33)	37.03 (28.22–45.29)
72	21.28 (14.61–28.59)	19.84 (10.22–29.57)	15.75 (2.81–26.37)	21.36 (10.21–32.5)	21.25 (7.03–34.33)	22.03 (6.56–36.95)	20.77 (6.4–33.72)	20.42 (7.45–33.07)
73	30.17 (25.33–37.09)	26.53 (19.38–33.02)	25.3 (18.14–31.82)	31.18 (24.17–39.11)	31.71 (24.53–40)	34.52 (21.17–45.87)	31.23 (21.96–39.68)	30.43 (22.9–37.79)
75	25.58 (20.06–31.76)	21.99 (15.89–28.3)	20.38 (15.14–27.38)	25.62 (18.48–32.11)	25.51 (18.18–33.31)	28.33 (15.6–38.41)	25.43 (16.58–33.82)	24.72 (17.18–31.97)
76	17.07 (8.84–24.53)	13.25 (4.01–22.55)	13.04 (4.42–21.37)	17.64 (7.53–27.84)	16.21 (4.59–26.51)	17.37 (4.56–29.24)	16 (4.71–26.41)	15.93 (5.36–26.72)
77	23.98 (18.52–29.93)	20.13 (14.57–25.68)	18.39 (11.55–23.88)	23.35 (16.46–29.7)	22.89 (15.22–30.14)	24.59 (14.6–32.98)	22.84 (14.56–30.6)	22.24 (15.14–29.55)
78	17.95 (13.04–23.22)	14.77 (10.24–19.68)	13.83 (7.16–18.39)	17.25 (11.93–22.5)	16.64 (10.38–23.24)	19.25 (9.47–27.02)	16.92 (9.77–23.57)	16.15 (10.16–22.87)
79	15.5 (11.07–20.6)	12.48 (7.83–17.26)	11.49 (6.52–15.82)	14.34 (8.66–19.25)	13.88 (8.07–19.7)	15.52 (7.03–22.54)	14.08 (7.7–19.9)	13.45 (7.95–19.45)
81	11.97 (7.86–16.14)	9.56 (5.51–14.7)	7.78 (4.57–11.68)	10.59 (5.41–15)	9.76 (4.87–15.15)	10.84 (4.23–16.63)	9.94 (4.84–14.92)	9.54 (4.95–14.49)
82	10.28 (6.53–14.31)	7.52 (3.74–12.3)	6.14 (3.28–9.67)	8.63 (3.97–13.07)	7.64 (3.06–12.59)	8.35 (2.86–13.75)	7.88 (3.11–12.65)	7.59 (3.24–12.41)

83	22.29 (17.04–28.17)	20.06 (14.64–25.74)	19.36 (13.76–25.16)	24.33 (16.69–30.71)	23.99 (17.06–31.16)	26.41 (14.95–36.1)	23.93 (15.85–31.17)	22.84 (16.23–29.95)
85	13.43 (8.75–19.89)	10.71 (6.97–15.06)	8.29 (3.39–13.54)	15.86 (9.51–22.26)	12.8 (6.4–19.97)	14.85 (5.34–22.94)	13.49 (6.21–21)	12.31 (6.01–18.96)
86	7.49 (4.2–11.3)	5.65 (3.01–8.78)	4.29 (0.83–8.12)	8.91 (4.57–13.9)	6.84 (2.38–12.2)	8.24 (2.05–13.9)	7.25 (2.21–12.53)	6.59 (2.33–11.76)
89	10.26 (6.22–14.11)	10.5 (4.93–15.88)	9.8 (4.67–15.46)	10.96 (5.46–17)	10.51 (4.67–17.46)	11.74 (3.82–18.6)	10.51 (4.57–17.27)	10.23 (4.49–16.49)
90	7.14 (4.03–10.53)	6.91 (2.62–12.12)	6.55 (2.21–11.58)	6.84 (3.01–11.84)	6.32 (1.85–11.57)	6.81 (1.89–12.55)	6.48 (1.76–11.62)	6.19 (1.64–11.11)
91	6.83 (4.19–10.2)	6.3 (3.2–10.15)	5.74 (2.01–11.05)	7.16 (2.84–11.24)	7.11 (2.27–13.02)	7.6 (2.03–14.12)	7.05 (1.98–12.67)	6.87 (2.31–12.36)
92	26.1 (19.22–32.55)	23.55 (16.47–29.94)	21.57 (10.15–34.7)	27.64 (18.08–36.74)	25.63 (13.3–38.34)	27.12 (12.27–40.55)	24.84 (12.81–36.17)	24.62 (13.59–35.63)
93	10.72 (6.73–15.11)	11.42 (4.57–18.64)	9.54 (2.55–18.61)	12.14 (5.55–18.27)	10.84 (3.95–19.34)	11.94 (3.55–21.54)	10.43 (3.96–18.29)	10.34 (3.82–17.88)
96	39.18 (29.91–50.43)	48.84 (35.02–63.28)	52.09 (34.79–70.52)	57.28 (38.53–76.88)	45.17 (29.35–62.71)	46.82 (27.03–66.3)	42.28 (26.46–57.88)	42.69 (27.01–57.45)
97	30.46 (21.55–40.14)	43.37 (30.88–60.24)	41.77 (18.27–56.47)	49.18 (33.12–68.12)	37.25 (22.57–52.46)	38.46 (21.85–55.37)	35.04 (21.93–50.12)	35.38 (22.55–50.16)
98	5.32 (1.83–8.53)	15.56 (7.77–22.18)	14.62 (4.37–26.77)	17.06 (7.12–26.99)	12.79 (4.29–22.53)	13.74 (4.25–24.98)	12.43 (4.43–22.13)	12.11 (4.25–21.54)
99	20.83 (13.98–28.32)	24.51 (12.02–37.96)	28.28 (11.59–47.12)	28.19 (14.6–43.05)	23.58 (12.45–35.93)	25.1 (12.59–39.3)	22.46 (12.11–33.98)	22.54 (12.53–34.08)
100	14.22 (8.73–19.29)	15.69 (7.95–23.07)	19.71 (9.05–30.24)	15.43 (10.11–21.57)	14.54 (8.19–22.21)	16.07 (8.11–24.08)	14.24 (7.82–20.97)	14.12 (8.04–20.88)
104	2.55 (0.64–4.64)	2.43 (0.26–5.84)	3.21 (0.21–8.68)	2.88 (0.55–5.89)	2.62 (0.24–5.97)	3.04 (0.2–6.49)	2.59 (0.28–5.78)	2.52 (0.27–5.67)
109	75.42 (63.87–88.28)	68.4 (54.66–81.03)	61.52 (43.65–75.85)	78.23 (65.05–96.71)	68.17 (54.06–81)	69.65 (53.31–83.38)	64.83 (50.77–77.11)	65.75 (52.04–78.17)
111	40.05 (28.16–54.08)	33.54 (15.81–57.18)	33.76 (13.92–53.08)	39.63 (18.38–61.13)	31.99 (10.91–53.52)	33.04 (12.16–55.75)	32.28 (13.87–52.55)	31.35 (12.65–51.96)
113	25.73 (17.47–35.04)	23.84 (10.95–36.61)	23.03 (11.54–37.84)	30.52 (14.79–44.37)	25 (11.88–39.4)	25.88 (10.43–42.97)	24.4 (11.97–37.76)	23.1 (10.99–36.07)
115	10.62 (4.68–16.99)	8.66 (2.84–17.72)	8.79 (2.46–17.16)	11.53 (3.04–24.27)	9.29 (1.89–18.09)	10.16 (2.07–19.72)	9.19 (2.21–17.47)	9.09 (2.13–17.36)
116	47.19 (34–62.26)	38.86 (26.23–54.57)	35.91 (22.6–58.65)	52.02 (33.13–72.02)	40.69 (24.48–57.71)	43.11 (23.81–62.28)	39.39 (24.74–54.76)	40.16 (24.66–56.56)
117	24.76 (16.38–34.43)	19.31 (10.68–30)	20.29 (7.19–43.03)	24.79 (11.5–39.75)	19.55 (8.22–32.26)	20.82 (6.79–35.45)	18.97 (7.63–31.49)	18.72 (7.37–30.85)
119	26.96 (17.37–38.01)	23.25 (13.05–38.25)	20.33 (10.31–35.19)	27.1 (11.91–44.99)	23.07 (10.52–37.62)	24.92 (10.06–40.87)	22.38 (10.27–35.22)	22.53 (9.75–35.73)
120	12.47 (7.21–18.88)	13.08 (3.97–29.7)	10.04 (2.52–17.41)	11.13 (3.58–22.62)	10.2 (2.82–19.09)	10.89 (2.63–20.58)	9.95 (2.73–18.47)	9.87 (2.99–18.07)
122	32.38 (25.33–39.63)	34.17 (22.82–47.73)	33.76 (19.89–50.92)	39.77 (27.2–53.21)	35.32 (24.33–47.35)	38.61 (22.73–55.05)	34.19 (23.32–46.33)	34.57 (23.34–46.47)
125	22.68 (16.86–30.21)	21.16 (14.22–30)	18.33 (8.67–32.5)	24.52 (14.62–32.88)	23.45 (14.55–33.31)	23.6 (11.96–35.21)	22.65 (13.88–32.32)	21.19 (12.5–30.2)
128	10.96 (5.39–16.28)	9.05 (3.99–14.65)	7.32 (1.76–14.85)	9.9 (3.85–16.68)	9.44 (2.74–17.17)	9.5 (2.36–17.57)	9.36 (2.91–17.29)	8.73 (2.47–15.92)
129	27.35 (21.36–34.62)	24.08 (17.26–33.5)	21.89 (12.62–35.94)	28.33 (19.3–39.31)	25.35 (16.46–35.28)	26.64 (15.16–38.1)	25.01 (15.86–34.78)	24.19 (15.28–33.43)
131	18.99 (14.2–24.76)	16.4 (9.89–24.5)	11.87 (4.89–20.06)	18.93 (10.56–28.22)	15.81 (6.82–24.09)	17.7 (7.02–28.8)	15.73 (7.56–24.41)	16.23 (7.99–25.79)
132	5.23 (2.36–8.49)	4.56 (1.27–9.15)	3.98 (0.58–9.06)	6.18 (1.69–12.56)	4.99 (1.12–9.89)	5.57 (1.03–11.03)	4.79 (1.12–9.51)	4.89 (1.09–9.65)

Node #	Node information, crown groups; fossil constraint	Node #	Node information, crown groups; fossil constraint	Node #	Node information, crown groups; fossil constraint
0	Monocot crown	6	Fossil constraint	28	Fossil constraint
1	Alismatales	7	Lemnoideae	29	Lasioideae
2	Araceae	13	Pothoideae; Fossil constraint	40	Zamioculcadoideae
3	Fossil constraint	16	Monsterioideae	41	Aroideae
4	Orontioideae	20	Fossil constraint	62	Fossil constraint

Table S5. Results for each node shown in Figure 3, with column 1 referring to node numbers, column 2 to clade support from posterior probability, column 3 to divergence time estimates with 95% confidence intervals (CI) in million years ago (Ma), column 4 to substitution rates as obtained from the program BEAST, column 5 to ancestral area reconstructions (AAR) using the program Lagrange without (w/o) extinct ranges from fossils included in the matrix, column 6 to reconstructions when fossils were included on short branches (see text for further explanation), column 7 to reconstructions when fossil were included on long branches, and column 8 to crown groups and their constraints. For details on the fossils see Table S2. In column 4, substitution rate is given for the branch to the left of the respective node, and in columns 5 to 7, ancestral areas are given for the branches descending from the respective node. Vertical bars separate upper branches (left) from lower branches (right). The areas coded are shown in the inset in Figure 3 and are: (A) Eurasia, (B) Africa, (C) Madagascar, Seychelles, and India, (D) Southeast Asia, (E) Australia, (F) North and Central America, (G) South America, (H) Antarctica, and (I) water-associated (free floating or in swamps) and widely distributed. Only AAR estimates with a probability of ≥5% are shown; estimates with a probability of >66.6% are shown in bold.

<table>
<tr><th>Node number (Fig. 3a,b)</th><th>Posterior Probability</th><th>Age (95% HPD) [Ma]</th><th>Rate (95% HPD) in [10^{-4} substitutions / site and Mys]</th><th>Ancestral area w/o fossils</th><th>Ancestral area with fossils on short branches</th><th>Ancestral area with fossils on long branches</th><th>Crown groups; age constraints with fossil names and minimum ages; fossils used for AAR with area code</th></tr>
<tr><td>0 (root)</td><td>1</td><td>137.76 (130.22–145.65)</td><td>N/A</td><td>N/A</td><td>N/A</td><td>N/A</td><td>Monocot crown</td></tr>
<tr><td>1</td><td>1</td><td>135.02 (125.79–143.54)</td><td>4.2 (0.4–10.4)</td><td>[FI|I] 20.9%
[GI|I] 14.2%
[FI|F] 12.2%
[F|EF] 7.0%
[I|AI] 6.0%</td><td>[FI|F] 17.8%
[FI|I] 13.5%
[F|EF] 10.4%
[GI|I] 9.0%
[F|F] 5.9%
[I|AI] 5.6%</td><td>[FI|F] 22.5%
[F|EF] 16.4%
[FI|I] 12.4%
[GI|I] 8.0%
[F|F] 6.9%
[F|FI] 6.9%</td><td>Alismatales</td></tr>
<tr><td>2</td><td>1</td><td>121.68 (112.01–131.9)</td><td>17.6 (8.9–27.7)</td><td>[I|I] 27.6%
[F|F] 11.1%
[A|AI] 10.8%
[EF|F] 6.9%
[I|AI] 5.3%</td><td>[F|F] 17.4%
[A|AI] 12.9%
[I|I] 12.8%
[EF|F] 10.7%
[F|FI] 7.2%</td><td>[F|F] 23.4%
[EF|F] 16.9%
[I|I] 15.2%
[F|FI] 10.1%</td><td>Araceae</td></tr>
</table>

3	1	95.58 (73.18–115.48)	3.6 (0.9–7.9)	[I|F] 17.3% [F|F] 11.4% [I|I] 10.4% [E|F] 7.7%	[F|F] 15.2% [I|F] 13.6% [E|F] 12.2% [DE|A] 6.5% [I|A] 6.5% [EF|F] 5.8% [G|F] 5.6%	[F|F] 22.6% [E|F] 18.7% [I|F] 16.5% [EF|F] 8.1% [G|F] 6.6%	Gymnostachydoideae; age constraint: *Albertarum pueri* (72 Ma)
4	1	52.81 (28.39–77.24)	6.6 (2.7–13)	[F|F] 47.5% [F|AF] 24.4% [F|A] 8.8% [FI|F] 6.5%	**[F|F] 76.0%** **[F|AF] 14.3%** **[F|A] 5.1%**	**[F|F] 86.7%** **[F|AF] 8.2%**	Orontioideae
5	1	20.6 (6.96–37.74)	5.9 (2.1–11)	[F|F] 40.0% [AF|F] 12.2% [F|AF] 12.2% [AF|A] 10.5% [A|AF] 10.5% [A|A] 8.0%	[F|F] 51.6% [AF|F] 10.5% [F|AF] 10.5% [AF|A] 9.0% [A|AF] 9.0%	[F|F] 58.7% [AF|F] 9.3% [F|AF] 9.3% [AF|A] 8.1% [A|AF] 8.1%	
6	1	103.55 (93–113.45)	21.9 (14–30.3)	[I|A] 43.3% [I|F] 14.1% [I|B] 7.0% [AI|A] 6.0%	[I|A] 30.9% [I|F] 21.7% [F|F] 5.0%	[I|F] 31.1% [I|A] 19.8% [F|F] 7.3%	Age constraint: *Limnobiophyllum scutatum* (65.5 Ma)
7	1	73.37 (59.46–87.91)	19.5 (11.4–27.8)	**[I|I] 77.4%** **[FI|I] 6.0%** **[AI|I] 5.2%**	**[I|I] 71.0%** **[FI|I] 9.1%** **[AI|I] 5.2%**	**[I|I] 70.5%** **[FI|I] 11.0%**	Lemnoideae
8	1	55.54 (41.4–70.36)	12.5 (5.3–22)	**[I|I] 95.7%**	**[I|I] 94.9%**	**[I|I] 95.2%**	
9	0.86	50.47 (36.61–64.91)	4.4 (0.7–10.2)	**[I|I] 99.1%**	**[I|I] 99.0%**	**[I|I] 99.1%**	
10	1	29.12 (18.33–40.48)	17.4 (9–27)	**[I|I] 99.8%**	**[I|I] 99.8%**	**[I|I] 99.8%**	
11	0.99	96.73 (86.62–107.06)	5.8 (1–12.4)	[A|A] 41.5% [A|AB] 18.5% [AFG|A] 9.5% [AF|A] 5.9%	[A|A] 28.5% [AFG|A] 18.7% [A|AB] 11.5% [FG|G] 7.1% [FG|A] 7.0% [FG|F] 5.2%	[AFG|A] 20.0% [A|A] 18.5% [FG|G] 10.8% [FG|F] 8.6% [A|AB] 8.1% [F|F] 8.0% [FG|A] 6.9%	

12	1	81.06 (68.3–93.68)	4.9 (1.5–9.8)	[A|A] 44.9% [A|AF] 7.2% [F|F] 5.9%	[A|A] 27.0% [AFG|F] 9.1% [FG|F] 7.0% [AFG|A] 6.6% [F|F] 5.3%	[A|A] 18.6% [AFG|F] 10.7% [FG|F] 9.8% [F|F] 8.2% [AFG|A] 7.5%	
13	1	64.51 (55.8–76.54)	4.7 (1.3–9.5)	[F|A] 22.3% [A|A] 21.7% [FG|A] 11.5% [A|D] 11.1% [A|AD] 10.7% [AF|A] 10.2%	[FG|A] 44.7% [F|A] 11.1% [A|A] 8.4% [AFG|A] 6.6% [AG|A] 6.4%	[FG|A] 49.4% [F|A] 10.9% [AFG|A] 6.8% [A|A] 6.7% [AG|A] 5.6%	Pothoideae; age constraint: *Petrocardium cerrejonense* (55.8 Ma)
14	1	26.13 (11.72–41.24)	3.9 (1.9–6.1)	[AD|D] 53.8% [A|D] 13.0% [D|D] 12.0% [ADE|D] 11.9%	[AD|D] 57.6% [A|D] 13.8% [ADE|D] 11.3% [D|D] 9.0%	[AD|D] 59.3% [A|D] 13.0% [ADE|D] 11.3% [D|D] 8.7%	
15	1	18.14 (6.62–31.62)	3.4 (0.5–7.7)	**[D|D] 97.6%**	**[D|D] 97.7%**	**[D|D] 97.9%**	
16	1	54.66 (47.03–63.99)	5.2 (2.3–8.8)	[F|A] 28.1% [F|AF] 24.4% [FG|A] 10.6% [A|A] 5.7% [F|AFG] 5.6% [AF|A] 5.3%	[F|A] 27.7% [F|AF] 23.3% [FG|A] 12.3% [F|AFG] 6.4% [F|F] 5.8%	[F|A] 24.7% [F|AF] 23.3% [FG|A] 12.4% [F|F] 8.2% [F|AFG] 7.0% [G|AFG] 5.1%	Monsteroideae
17	1	31.5 (17.92–47.05)	2.4 (0.8–4.9)	[F|F] 52.0% [FG|F] 11.8% [F|FG] 7.2% [FG|G] 7.1% [G|FG] 5.8%	[F|F] 51.4% [FG|F] 12.6% [F|FG] 7.7% [FG|G] 7.6% [G|FG] 6.2%	[F|F] 51.3% [FG|F] 12.7% [FG|G] 8.2% [F|FG] 7.8% [G|FG] 6.5% [G|G] 5.5%	
18	1	22.61 (10.34–36.36)	2.6 (0.4–6.3)	[F|F] 60.9% [G|G] 9.9% [FG|F] 8.7% [FG|G] 6.5% [F|FG] 6.1% [G|FG] 5.1%	[F|F] 59.7% [G|G] 10.6% [FG|F] 9.0% [FG|G] 6.7% [F|FG] 6.3% [G|FG] 5.3%	[F|F] 58.7% [G|G] 11.7% [FG|F] 9.0% [FG|G] 6.9% [F|FG] 6.4% [G|FG] 5.4%	

19	1	16.21 (5.16–28.31)	2.7 (0.4–6.6)	[F|F] 56.8% [G|G] 12.6% [FG|F] 7.9% [F|FG] 7.9% [FG|G] 6.9% [G|FG] 6.9%	[F|F] 55.9% [G|G] 13.2% [FG|F] 8.0% [F|FG] 8.0% [FG|G] 7.0% [G|FG] 7.0%	[F|F] 54.9% [G|G] 14.3% [FG|F] 8.0% [F|FG] 8.0% [FG|G] 7.1% [G|FG] 7.1%	
20	0.81	51.38 (47–59.35)	3.1 (0.4–7.4)	[A|A] 46.6% [AF|A] 20.9% [AFG|A] 9.4% [F|A] 5.7%	[A|A] 46.8% [AF|A] 23.3% [AFG|A] 11.7% [F|A] 6.5%	[A|A] 42.5% [AF|A] 23.8% [AFG|A] 13.0% [F|A] 6.4%	Age constraint: *Araciphyllites tertiarius* (47 Ma)
21	1	27.69 (16.29–40.77)	1.5 (0.5–2.9)	**[A|A] 84.8%** **[A|AF] 5.0%**	**[A|A] 89.4%**	**[A|A] 89.1%**	
22	0.98	23.14 (12.16–35.29)	2.8 (0.4–6.7)	**[A|A] 69.7%** **[A|AF] 12.3%** **[AD|A] 6.6%**	**[A|A] 73.1%** **[A|AF] 11.0%** **[AD|A] 6.3%**	**[A|A] 73.3%** **[A|AF] 11.3%** **[AD|A] 6.1%**	
23	1	17.91 (8.34–28.8)	3.1 (0.5–7.2)	[F|A] 46.8% [A|A] 26.2% [FG|A] 13.7%	[F|A] 49.3% [A|A] 25.3% [FG|A] 13.6%	[F|A] 49.6% [A|A] 25.2% [FG|A] 13.7%	
24	1	10.93 (3.72–19.71)	3.1 (0.5–7.1)	[A|A] 49.7% [AD|D] 10.6% [AD|A] 9.8% [D|AD] 8.1% [A|AD] 7.7%	[A|A] 50.2% [AD|D] 10.6% [AD|A] 9.7% [D|AD] 8.1% [A|AD] 7.6%	[A|A] 51.4% [AD|D] 10.4% [AD|A] 9.6% [D|AD] 7.9% [A|AD] 7.5%	
25	0.98	21.99 (10.74–34.89)	2.4 (0.4–6.1)	**[A|A] 70.3%** **[A|AB] 7.5%** **[AD|D] 6.3%** **[AD|A] 5.5%**	**[A|A] 71.4%** **[A|AB] 7.9%** **[AD|D] 6.4%** **[AD|A] 5.5%**	**[A|A] 72.7%** **[A|AB] 7.8%** **[AD|D] 6.0%** **[AD|A] 5.3%**	
26	1	12.15 (3.34–22.39)	2.9 (0.5–6.4)	[B|A] 64.5% [B|D] 9.1% [A|A] 7.6%	**[B|A] 67.6%** **[B|D] 8.3%** **[A|A] 7.0%**	**[B|A] 68.9%** **[B|D] 8.0%** **[A|A] 7.1%**	
27	1	21.05 (6.7–36.42)	3.3 (1.3–5.9)	[A|F] 29.9% [A|FG] 24.0% [D|A] 22.2% [A|A] 7.2%	[A|F] 30.9% [A|FG] 27.7% [D|A] 21.0% [A|A] 6.3%	[A|F] 30.6% [A|FG] 29.1% [D|A] 19.2% [A|A] 5.8%	

28	1	90.23 (80.09–100.68)	4.9 (0.9–10.6)	**[A|AB] 80.2%** **[FG|G] 6.5%** **[A|B] 5.8%**	[A|AB] 53.5% [A|B] 21.5% [FG|G] 15.5%	[A|AB] 43.6% [FG|G] 24.9% [A|B] 17.5%	Age constraint: *Lasioideaecidites hessei* (70 Ma)
29	1	26.38 (15–37.84)	3.2 (2.1–4.5)	[F|AFG] 35.1% [G|AFG] 28.3% [F|AF] 20.6%	[F|AFG] 27.8% [F|AF] 27.5% [G|AFG] 22.6% [F|F] 6.1%	[F|AFG] 28.8% [F|AF] 24.1% [G|AFG] 23.9% [F|F] 6.9%	Lasioideae
30	0.39	24.17 (14.08–35.15)	2.5 (0.3–6.4)	**[FG|A] 68.8%** **[F|A] 17.2%**	[FG|A] 59.9% [F|A] 27.0%	[FG|A] 62.5% [F|A] 25.1%	
31	0.89	19.48 (10.86–28.52)	3 (0.4–7.1)	**[D|AD] 75.3%** **[D|A] 13.4%** **[A|A] 9.1%**	**[D|AD] 76.5%** **[D|A] 13.4%** **[A|A] 8.0%**	**[D|AD] 78.0%** **[D|A] 12.5%** **[A|A] 7.5%**	
32	0.23	18.14 (10.25–26.98)	2.9 (0.4–7.2)	[D|A] 40.4% [AD|A] 37.7% [A|A] 20.4%	[D|A] 40.8% [AD|A] 38.4% [A|A] 19.4%	[AD|A] 40.8% [D|A] 39.7% [A|A] 18.3%	
33	0.64	15.18 (7.58–24.37)	2.9 (0.4–6.9)	**[A|A] 90.3%** **[A|AB] 8.5%**	**[A|A] 90.3%** **[A|AB] 8.7%**	**[A|A] 90.5%** **[A|AB] 8.5%**	
34	0.78	10.02 (2.77–17.97)	4.3 (0.5–9.6)	**[B|A] 79.6%** **[A|A] 13.1%**	**[B|A] 81.6%** **[A|A] 11.8%**	**[B|A] 82.1%** **[A|A] 11.7%**	
35	0.64	14.88 (6.84–23.94)	2.9 (0.4–6.9)	[AD|D] 47.4% [D|D] 40.0% [A|D] 9.4%	[AD|D] 47.7% [D|D] 40.3% [A|D] 9.3%	[AD|D] 49.7% [D|D] 39.2% [A|D] 8.8%	
36	1	16.3 (6.62–26.5)	2.6 (0.4–6.2)	**[FG|G] 89.0%** **[AFG|G] 5.6%**	**[FG|G] 90.0%** **[AFG|G] 5.2%**	**[FG|G] 90.8%**	
37	0.65	13.87 (5.13–23.72)	2.8 (0.4–6.8)	**[G|G] 99.8%**	**[G|G] 99.8%**	**[G|G] 99.8%**	
38	0.79	86.95 (77.1–97.03)	3.8 (0.5–8.7)	**[B|AB] 84.6%** **[B|BG] 7.9%** **[B|B] 6.5%**	[B|AB] 54.4% [B|B] 23.5% [B|BG] 21.3%	[B|AB] 44.7% [B|BG] 32.9% [B|B] 21.5%	
39	1	66.95 (41.1–86.91)	2.3 (0.4–5.7)	**[B|B] 99.5%**	**[B|B] 99.3%**	**[B|B] 99.4%**	
40	1	22.73 (5.69–41.84)	3.2 (1.3–6.1)	**[B|B] 98.6%**	**[B|B] 98.8%**	**[B|B] 99.0%**	Zamioculcadoideae
41	1	82.12 (73.24–92.28)	5.1 (1–10.5)	**[B|AB] 84.9%** **[B|BG] 7.9%** **[B|B] 6.1%**	[B|AB] 54.4% [B|BG] 22.9% [B|B] 21.7%	[B|AB] 44.7% [B|BG] 34.2% [B|B] 19.9%	Aroideae
42	0.72	80.03 (71.23–89.77)	3.6 (0.5–8.3)	**[B|AB] 85.2%** **[B|BG] 8.0%**	[B|AB] 54.5% [B|BG] 27.3% [B|B] 15.9%	[B|AB] 44.8% [B|BG] 38.2% [B|B] 14.6%	

<table>
<tr><td>43</td><td>0.65</td><td>79.08 (70.33–87.78)</td><td>3.7 (0.5–8.6)</td><td>**[AB|A] 83.2%**
[BG|G] 9.0%</td><td>[AB|A] 53.3%
[BG|G] 41.0%</td><td>[BG|G] 51.0%
[AB|A] 44.0%</td><td></td></tr>
<tr><td>44</td><td>0.33</td><td>77.88 (69.49–86.65)</td><td>3.5 (0.4–8.4)</td><td>**[A|A] 84.5%**
[G|G] 8.6%</td><td>[A|A] 49.7%
[G|G] 40.2%
[G|AG] 5.3%</td><td>[G|G] 50.0%
[A|A] 40.4%
[G|AG] 5.5%</td><td>Age constraint:
Montrichardia aquatica
(55.8 Ma)</td></tr>
<tr><td>45</td><td>0.91</td><td>76.06 (67.72–84.35)</td><td>4.2 (0.7–9.8)</td><td>**[A|A] 80.4%**
[D|A] 5.5%
[G|G] 5.3%</td><td>[A|A] 48.0%
[G|G] 24.8%
[AG|A] 12.9%</td><td>[A|A] 39.5%
[G|G] 30.5%
[AG|A] 16.1%
[G|AG] 5.0%</td><td></td></tr>
<tr><td>46</td><td>0.7</td><td>73.8 (66.32–81.88)</td><td>4.4 (0.8–9.9)</td><td>**[A|A] 88.0%**
[A|AG] 5.5%</td><td>[A|A] 65.1%
[A|AG] 26.1%</td><td>[A|A] 59.3%
[A|AG] 32.6%</td><td></td></tr>
<tr><td>47</td><td>1</td><td>66.18 (60.34–72.84)</td><td>13.5 (5.5–24.1)</td><td>**[A|A] 84.1%**
[AG|A] 7.4%</td><td>[A|A] 63.5%
[AG|A] 29.0%</td><td>[A|A] 58.3%
[AG|A] 35.5%</td><td></td></tr>
<tr><td>48</td><td>1</td><td>58.49 (47.42–68.23)</td><td>3 (0.6–7)</td><td>**[A|A] 68.7%**
[A|AG] 13.3%</td><td>[A|A] 51.6%
[A|AG] 31.1%</td><td>[A|A] 48.5%
[A|AG] 37.1%</td><td></td></tr>
<tr><td>49</td><td>1</td><td>24.17 (9.76–40.43)</td><td>3.2 (1.5–5.6)</td><td>[A|A] 63.9%
[A|AB] 19.9%</td><td>[A|A] 64.2%
[A|AB] 20.5%</td><td>[A|A] 66.3%
[A|AB] 20.8%</td><td></td></tr>
<tr><td>50</td><td>0.49</td><td>20.98 (8.5–36.72)</td><td>2.7 (0.3–6.6)</td><td>[A|B] 40.5%
[A|A] 34.3%</td><td>[A|B] 43.2%
[A|A] 32.9%</td><td>[A|B] 45.1%
[A|A] 33.6%</td><td></td></tr>
<tr><td>51</td><td>1</td><td>42.02 (30.47–54.14)</td><td>4.6 (1.6–8.9)</td><td>**[AG|G] 80.6%**
[DG|G] 7.7%</td><td>**[AG|G] 81.7%**
[DG|G] 6.3%</td><td>**[AG|G] 85.0%**</td><td></td></tr>
<tr><td>52</td><td>0.96</td><td>34.24 (18.88–49.35)</td><td>2.3 (0.4–5.8)</td><td>**[A|G] 71.2%**
[A|AG] 8.7%
[D|G] 7.2%</td><td>**[A|G] 73.6%**
[A|AG] 8.0%
[D|G] 6.7%</td><td>**[A|G] 76.4%**
[A|AG] 8.0%
[D|G] 5.4%</td><td></td></tr>
<tr><td>53</td><td>1</td><td>37.62 (26.7–48.81)</td><td>3.3 (0.5–7.7)</td><td>**[G|G] 90.5%**
[FG|G] 7.3%</td><td>**[G|G] 91.0%**
[FG|G] 7.2%</td><td>**[G|G] 92.2%**
[FG|G] 6.3%</td><td></td></tr>
<tr><td>54</td><td>1</td><td>20.28 (7.2–34.13)</td><td>2.4 (0.6–5.3)</td><td>[G|G] 62.6%
[FG|F] 9.5%
[F|FG] 9.5%
[FG|G] 8.1%
[G|FG] 8.1%</td><td>[G|G] 62.9%
[FG|F] 9.5%
[F|FG] 9.5%
[FG|G] 8.1%
[G|FG] 8.1%</td><td>[G|G] 64.7%
[FG|F] 9.1%
[F|FG] 9.1%
[FG|G] 7.9%
[G|FG] 7.9%</td><td></td></tr>
<tr><td>55</td><td>1</td><td>32.08 (22.18–42.91)</td><td>4.1 (0.8–9.3)</td><td>**[G|G] 98.3%**</td><td>**[G|G] 98.4%**</td><td>**[G|G] 98.6%**</td><td></td></tr>
<tr><td>56</td><td>1</td><td>13.64 (4.55–23.39)</td><td>5 (1.8–9.6)</td><td>**[G|G] 98.5%**</td><td>**[G|G] 98.7%**</td><td>**[G|G] 99.0%**</td><td></td></tr>
<tr><td>57</td><td>0.71</td><td>30.02 (20–40.56)</td><td>3 (0.4–7.1)</td><td>**[G|G] 97.2%**</td><td>**[G|G] 97.3%**</td><td>**[G|G] 97.5%**</td><td></td></tr>
<tr><td>58</td><td>1</td><td>16.74 (7.9–26.57)</td><td>5 (1.6–9.7)</td><td>**[G|G] 98.7%**</td><td>**[G|G] 98.9%**</td><td>**[G|G] 99.1%**</td><td></td></tr>
<tr><td>59</td><td>1</td><td>6.49 (1.44–12.65)</td><td>5.3 (1.5–10.7)</td><td>**[G|G] 99.5%**</td><td>**[G|G] 99.6%**</td><td>**[G|G] 99.7%**</td><td></td></tr>
</table>

60	1	16.87 (7.23–27.34)	4.8 (1.6–9.3)	[G|G] 56.5% [FG|F] 11.4% [F|FG] 11.4% [FG|G] 9.9% [G|FG] 9.9%	[G|G] 56.6% [FG|F] 11.4% [F|FG] 11.4% [FG|G] 9.9% [G|FG] 9.9%	[G|G] 57.8% [FG|F] 11.0% [F|FG] 11.0% [FG|G] 9.7% [G|FG] 9.7%	
61	1	62.25 (57.77–67.78)	6.4 (1.3–13.5)	**[A|A] 88.7%**	**[A|A] 92.0%**	**[A|A] 92.6%**	
62	1	57.46 (55.8–60.67)	6.9 (1.7–14)	**[A|A] 84.1%** **[A|AC] 8.4%**	**[A|A] 93.9%**	**[A|A] 93.4%**	Age constraint: *Nitophyllites zaisanicus* (55.8 Ma)
63	1	29.57 (12.46–47.42)	3 (1.1–6.1)	**[A|A] 95.1%**	**[A|A] 94.9%**	**[A|A] 95.3%**	
64	1	38.85 (20.53–56.28)	1.3 (0.3–3.5)	**[A|C] 90.6%**	**[A|C] 92.7%**	**[A|C] 92.3%**	
65	1	29.27 (13.89–48.71)	2 (0.3–5.2)	**[C|C] 97.7%**	**[C|C] 97.9%**	**[C|C] 98.0%**	
66	1	21.27 (7.75–38.52)	2.6 (0.4–6.3)	**[C|C] 99.1%**	**[C|C] 99.2%**	**[C|C] 99.3%**	
67	1	3.68 (0.32–8.34)	3 (0.8–6.1)	**[C|C] 99.8%**	**[C|C] 99.8%**	**[C|C] 99.9%**	
68	1	45.68 (35.09–55.26)	5.3 (2.2–9.7)	[C|A] 54.6% [A|A] 19.1% [I|A] 11.1% [AC|A] 7.6%	[C|A] 55.9% [A|A] 18.3% [I|A] 11.6% [AC|A] 7.2%	[C|A] 55.5% [A|A] 19.4% [I|A] 11.5% [AC|A] 7.1%	
69	1	38.97 (30.17–48.2)	3.7 (0.6–8.3)	**[A|A] 91.8%**	**[A|A] 92.1%**	**[A|A] 93.2%**	
70	0.35	37.23 (28.59–46.04)	3 (0.4–7.1)	**[A|A] 97.9%**	**[A|A] 98.1%**	**[A|A] 98.5%**	
71	0.99	34.68 (26.8–43.13)	3.6 (0.5–8.4)	**[A|A] 97.3%**	**[A|A] 97.4%**	**[A|A] 97.6%**	
72	1	21.25 (7.03–34.33)	2 (0.4–4.8)	**[A|A] 77.6%** **[AD|A] 11.6%**	**[A|A] 77.8%** **[AD|A] 11.6%**	**[A|A] 79.0%** **[AD|A] 11.1%**	
73	1	31.71 (24.53–40)	4.1 (0.6–9.3)	**[A|A] 97.1%**	**[A|A] 97.0%**	**[A|A] 97.2%**	
74	0.38	30.3 (22.87–38.45)	2.7 (0.4–6.7)	**[A|A] 98.8%**	**[A|A] 98.8%**	**[A|A] 98.9%**	
75	1	25.51 (18.18–33.31)	3.7 (0.7–8.4)	**[A|A] 88.8%** **[AE|A] 7.0%**	**[A|A] 88.7%** **[AE|A] 7.1%**	**[A|A] 89.2%** **[AE|A] 7.1%**	
76	0.99	16.21 (4.59–26.51)	2.3 (0.4–5.6)	**[E|A] 73.5%** **[A|A] 14.6%**	**[E|A] 75.9%** **[A|A] 13.3%**	**[E|A] 76.5%** **[A|A] 13.5%**	
77	0.95	22.89 (15.22–30.14)	3.4 (0.5–7.8)	**[A|A] 89.0%**	**[A|A] 89.0%**	**[A|A] 89.7%**	
78	1	16.64 (10.38–23.24)	5.6 (1.4–11.9)	**[A|A] 86.9%** **[AD|A] 10.3%**	**[A|A] 87.0%** **[AD|A] 10.2%**	**[A|A] 87.9%** **[AD|A] 9.7%**	
79	0.96	13.88 (8.07–19.7)	3.5 (0.5–8.2)	**[A|A] 99.4%**	**[A|A] 99.4%**	**[A|A] 99.5%**	
80	0.9	12.07 (6.67–17.55)	3.1 (0.3–7.3)	**[A|A] 98.6%**	**[A|A] 98.7%**	**[A|A] 98.7%**	

81	1	9.76 (4.87–15.15)	3.6 (0.5–8.2)	**[A|A] 92.2%** **[AB|A] 5.3%**	**[A|A] 92.2%** **[AB|A] 5.3%**	**[A|A] 92.4%** **[AB|A] 5.1%**
82	0.96	7.64 (3.06–12.59)	3.3 (0.3–7.5)	**[A|A] 92.4%** **[A|AB] 7.5%**	**[A|A] 92.4%** **[A|AB] 7.5%**	**[A|A] 92.6%** **[A|AB] 7.3%**
83	1	23.99 (17.06–31.16)	6.3 (1.7–13.1)	**[A|A] 79.7%** **[A|AD] 16.8%**	**[A|A] 78.8%** **[A|AD] 17.8%**	**[A|A] 79.2%** **[A|AD] 17.7%**
84	0.84	17.65 (11.03–24.58)	4.2 (0.8–9.2)	**[A|A] 95.5%**	**[A|A] 95.6%**	**[A|A] 95.9%**
85	1	12.8 (6.4–19.97)	4.5 (0.9–9.6)	**[A|A] 83.2%** **[A|AB] 16.4%**	**[A|A] 83.2%** **[A|AB] 16.5%**	**[A|A] 83.6%** **[A|AB] 16.1%**
86	1	6.84 (2.38–12.2)	5.5 (1.2–11.7)	**[B|A] 90.0%** **[A|A] 5.2%**	**[B|A] 91.1%**	**[B|A] 91.3%**
87	0.33	21.9 (15.12–29.2)	2.9 (0.4–7)	[A|A] 50.2% [D|A] 40.8%	[A|A] 47.7% [D|A] 43.9%	[A|A] 47.9% [D|A] 44.1%
88	0.81	18.54 (11.68–25.96)	3.3 (0.5–7.5)	[A|A] 61.6% [AF|F] 16.7% [F|AF] 6.3% [A|AF] 5.7%	[A|A] 61.9% [AF|F] 16.7% [F|AF] 6.3% [A|AF] 5.7%	[A|A] 62.9% [AF|F] 16.6% [F|AF] 6.1% [A|AF] 5.6%
89	1	10.51 (4.67–17.46)	3.1 (0.6–6.8)	**[F|AF] 77.2%** **[F|F] 16.2%** **[F|A] 5.5%**	**[F|AF] 77.7%** **[F|F] 16.0%** **[F|A] 5.4%**	**[F|AF] 78.8%** **[F|F] 15.5%**
90	1	6.32 (1.85–11.57)	3.6 (0.6–8.3)	**[F|A] 94.3%**	**[F|A] 94.9%**	**[F|A] 95.1%**
91	1	7.11 (2.27–13.02)	5.5 (1.9–10.3)	**[F|A] 93.1%**	**[F|A] 93.8%**	**[F|A] 93.9%**
92	1	25.63 (13.3–38.34)	2.8 (0.5–6.4)	**[A|A] 81.1%** **[AD|A] 5.2%**	**[A|A] 81.3%** **[AD|A] 5.1%**	**[A|A] 83.1%**
93	1	10.84 (3.95–19.34)	2.7 (0.8–5.9)	[A|A] 54.6% [AD|A] 24.7% [D|AD] 6.9% [A|AD] 6.3%	[A|A] 54.7% [AD|A] 24.7% [D|AD] 6.9% [A|AD] 6.3%	[A|A] 57.1% [AD|A] 23.9% [D|AD] 6.5% [A|AD] 6.0%
94	0.8	7.75 (2.12–14.96)	2.9 (0.4–6.9)	**[A|A] 76.7%** **[AD|A] 20.5%**	**[A|A] 76.8%** **[AD|A] 20.5%**	**[A|A] 77.9%** **[AD|A] 19.8%**
95	0.73	38.9 (23.8–51.71)	2.5 (0.3–6.2)	[C|C] 36.8% [C|I] 19.6% [C|A] 11.3% [I|I] 7.7% [A|I] 5.9% [A|A] 5.2%	[C|C] 35.9% [C|I] 21.8% [C|A] 11.3% [I|I] 7.7% [A|I] 6.0%	[C|C] 35.4% [C|I] 22.1% [C|A] 11.8% [I|I] 7.5% [A|I] 6.1%

96	1	45.17 (29.35–62.71)	4.7 (1.9–8.9)	[G|A] 17.7% [A|D] 14.9% [D|AD] 13.7% [G|D] 10.8% [D|D] 8.7% [A|AD] 8.4% [A|A] 5.8%	[G|D] 28.3% [G|A] 22.4% [A|D] 8.8% [D|AD] 8.2% [DG|D] 5.3% [A|AD] 5.0%	[G|D] 33.1% [G|A] 24.5% [A|D] 7.1% [D|AD] 6.6% [DG|D] 5.7%
97	0.99	37.25 (22.57–52.46)	3.2 (0.5–7.3)	[AD|D] 42.3% [D|D] 39.5% [A|D] 14.6%	[D|D] 47.9% [AD|D] 36.2% [A|D] 12.4%	[D|D] 49.7% [AD|D] 35.5% [A|D] 11.4%
98	1	12.79 (4.29–22.53)	10.3 (4.7–17.5)	[D|D] 19.2% [AD|D] 17.8% [D|AD] 17.8% [AD|A] 16.1% [A|AD] 16.1% [A|A] 6.7%	[D|D] 23.1% [AD|D] 17.1% [D|AD] 17.1% [AD|A] 15.5% [A|AD] 15.5% [A|A] 5.6%	[D|D] 24.3% [AD|D] 16.9% [D|AD] 16.9% [AD|A] 15.5% [A|AD] 15.5% [A|A] 5.4%
99	1	23.58 (12.45–35.93)	2.4 (0.5–5.5)	**[D|D] 97.5%**	**[D|D] 97.8%**	**[D|D] 98.0%**
100	1	14.54 (8.19–22.21)	3.4 (0.6–7.5)	**[D|D] 99.4%**	**[D|D] 99.5%**	**[D|D] 99.5%**
101	0.25	13.13 (7.26–19.56)	2.9 (0.3–7.2)	**[D|D] 99.7%**	**[D|D] 99.8%**	**[D|D] 99.8%**
102	0.19	11.48 (6.29–17.11)	2.7 (0.4–6.6)	**[D|D] 99.5%**	**[D|D] 99.5%**	**[D|D] 99.6%**
103	0.17	8.72 (3.51–13.95)	2.8 (0.4–6.5)	**[D|D] 96.9%**	**[D|D] 96.9%**	**[D|D] 97.0%**
104	1	2.62 (0.24–5.97)	3 (0.7–6.2)	**[D|D] 67.6%** **[D|AD] 31.1%**	**[D|D] 67.6%** **[D|AD] 31.1%**	**[D|D] 68.0%** **[D|AD] 30.9%**
105	0.49	6.53 (1.7–11.79)	2.9 (0.4–7)	**[D|D] 100.0%**	**[D|D] 100.0%**	**[D|D] 100.0%**
106	0.85	8.61 (3.96–13.73)	2.9 (0.4–6.9)	**[D|D] 100.0%**	**[D|D] 100.0%**	**[D|D] 100.0%**
107	0.84	6.42 (2.31–10.67)	3.2 (0.4–7.6)	**[D|D] 100.0%**	**[D|D] 100.0%**	**[D|D] 100.0%**
108	0.18	5.43 (1.88–9.43)	3.1 (0.3–7.5)	**[D|D] 100.0%**	**[D|D] 100.0%**	**[D|D] 100.0%**
109	1	68.17 (54.06–81)	2.4 (0.4–5.7)	**[AB|B] 83.9%** **[B|BG] 6.9%** **[B|B] 5.2%**	[AB|B] 53.7% [B|BG] 30.2% [BG|G] 8.5%	[AB|B] 44.4% [B|BG] 38.4% [BG|G] 10.0%
110	0.69	63.18 (49.44–78.02)	2.4 (0.3–5.8)	**[B|AB] 83.7%** **[B|B] 10.8%**	[B|AB] 56.7% [B|B] 30.6% [B|BG] 8.5%	[B|AB] 48.4% [B|B] 37.1% [B|BG] 10.1%
111	1	31.99 (10.91–53.52)	2.3 (0.6–4.8)	**[B|B] 99.3%**	**[B|B] 99.3%**	**[B|B] 99.5%**

112	0.62	59.32 (44.86–74.51)	2.6 (0.4–6.4)	**[A|AB] 87.3%**	**[A|AB] 72.9%** **[D|BD] 8.9%** **[G|B] 8.4%**	**[A|AB] 68.6%** **[D|BD] 11.6%** **[G|B] 9.9%**
113	1	25 (11.88–39.4)	4 (1.8–6.9)	[F|AF] 54.4% [F|AFG] 7.6% [F|A] 7.3% [G|AFG] 6.2% [A|A] 5.2%	[F|AF] 46.6% [F|AFG] 7.3% [G|AFG] 6.0% [F|A] 5.9% [F|DF] 5.0%	[F|AF] 44.8% [F|AFG] 7.1% [F|DF] 6.5% [G|AFG] 6.0% [G|DG] 5.2%
114	0.89	20.5 (9.17–33.21)	2.9 (0.4–6.9)	[F|A] 49.0% [FG|A] 28.4% [A|A] 6.9% [AF|A] 5.4%	[F|A] 43.8% [FG|A] 29.5% [A|A] 5.1%	[F|A] 41.9% [FG|A] 29.6% [F|D] 6.3% [G|D] 6.1%
115	1	9.29 (1.89–18.09)	3.9 (0.9–8.5)	**[AD|D] 82.6%** **[A|D] 11.1%**	**[AD|D] 78.3%** **[A|D] 10.4%** **[D|D] 9.8%**	**[AD|D] 77.3%** **[D|D] 12.1%** **[A|D] 9.2%**
116	1	40.69 (24.48–57.71)	2.8 (0.7–5.8)	**[A|B] 83.0%** **[D|B] 8.7%**	**[A|B] 70.7%** **[D|B] 20.9%**	**[A|B] 66.9%** **[D|B] 25.0%**
117	1	19.55 (8.22–32.26)	3 (0.9–6.4)	**[AD|D] 69.5%** **[A|D] 16.8%** **[D|D] 10.6%**	[AD|D] 60.7% [D|D] 22.1% [A|D] 14.5%	[AD|D] 58.9% [D|D] 25.8% [A|D] 12.8%
118	0.82	14.1 (4.04–25.84)	2.5 (0.3–6)	**[D|D] 98.1%**	**[D|D] 98.4%**	**[D|D] 98.6%**
119	1	23.07 (10.52–37.62)	3.6 (0.9–7.8)	**[B|B] 95.5%**	**[B|B] 95.9%**	**[B|B] 96.4%**
120	1	10.2 (2.82–19.09)	4.7 (1.2–10.1)	**[B|B] 98.8%**	**[B|B] 98.9%**	**[B|B] 99.1%**
121	0.77	61.92 (47.25–76.14)	3 (0.4–7.3)	[B|B] 56.5% [B|G] 27.8% [BG|G] 6.8%	[B|G] 38.6% [B|B] 35.2% [G|G] 11.6% [BG|G] 8.4%	[B|G] 43.2% [B|B] 28.5% [G|G] 13.4% [BG|G] 8.8%
122	1	35.32 (24.33–47.35)	6.1 (2.8–11)	**[G|G] 67.3%** **[BG|G] 21.1%** **[G|BG] 5.4%**	**[G|G] 78.3%** **[BG|G] 13.9%**	**[G|G] 82.8%** **[BG|G] 11.2%**
123	0.59	32.69 (23.06–44.08)	3.1 (0.4–7.3)	**[G|G] 94.8%**	**[G|G] 96.5%**	**[G|G] 97.2%**
124	0.78	29.07 (19.97–38.95)	3.5 (0.5–8)	**[G|G] 99.3%**	**[G|G] 99.4%**	**[G|G] 99.5%**
125	1	23.45 (14.55–33.31)	3.5 (0.6–7.9)	**[G|G] 99.3%**	**[G|G] 99.4%**	**[G|G] 99.5%**
126	0.77	19.55 (11.38–28.23)	3.5 (0.5–8)	**[G|G] 99.7%**	**[G|G] 99.7%**	**[G|G] 99.8%**

127	0.71	15.7 (7.67–24.54)	3.4 (0.4–7.9)	**[G|G] 99.6%**	**[G|G] 99.6%**	**[G|G] 99.7%**	
128	1	9.44 (2.74–17.17)	3.8 (1–7.9)	**[G|G] 99.4%**	**[G|G] 99.5%**	**[G|G] 99.6%**	
129	0.98	25.35 (16.46–35.28)	3.2 (0.4–7.4)	**[G|G] 96.4%**	**[G|G] 96.4%**	**[G|G] 96.6%**	
130	0.69	22.37 (13.59–31.89)	3.1 (0.4–7.5)	**[G|G] 99.6%**	**[G|G] 99.7%**	**[G|G] 99.7%**	
131	1	15.81 (6.82–24.09)	4.1 (0.8–8.7)	**[G|G] 99.4%**	**[G|G] 99.5%**	**[G|G] 99.6%**	
132	1	4.99 (1.12–9.89)	5.2 (1.7–10.9)	**[G|G] 99.7%**	**[G|G] 99.7%**	**[G|G] 99.8%**	
fos1	N/A	72	N/A	#N/A	**[F|AF] 72.5%** **[F|F] 21.7%** **[F|A] 5.6%**	**[F|F] 77.8%** **[F|AF] 9.3%**	*Albertarum pueri* (F)
fos2	N/A	70	N/A	#N/A	**[A|F] 84.0%** **[A|AF] 12.2%**	**[F|F] 84.0%** **[A|F] 7.7%**	*Lysichiton austriacus* (A)
fos3	N/A	66	N/A	#N/A	**[F|F] 84.7%** **[F|AF] 12.6%**	**[F|F] 95.1%**	*Orontium mackii* (F)
fos4	N/A	56	N/A	#N/A	[G|FG] 57.1% [G|AG] 18.7% [G|AFG] 14.1% [G|G] 8.9%	[G|FG] 61.4% [G|AG] 14.2% [G|AFG] 12.3% [G|G] 9.3%	*Petrocardium cerrejonense* (G)
fos5	N/A	47	N/A	#N/A	**[A|A] 95.0%**	**[A|A] 91.4%**	*Araciphyllites tertiarius* (A)
fos6	N/A	70	N/A	#N/A	[A|A] 42.9% [A|AF] 17.0% [A|AFG] 14.9% [A|F] 12.8% [A|FG] 7.7%	[A|A] 31.2% [A|AFG] 13.9% [A|AF] 11.1% [A|F] 7.5% [F|FG] 7.3% [A|FG] 6.5%	*Lasioideaecidites hessei* (A)
fos7	N/A	49	N/A	#N/A	[F|AFG] 42.6% [F|AF] 36.2% [F|F] 9.0% [F|AG] 5.4%	[F|AFG] 43.0% [F|AF] 29.0% [F|F] 9.0% [F|FG] 6.7%	*Keratosperma allenbyense* (F)
fos8	N/A	59	N/A	#N/A	[G|G] 43.7% [AG|G] 24.1% [AFG|G] 22.0% [FG|G] 9.3%	[G|G] 52.5% [AG|G] 19.6% [AFG|G] 16.8% [FG|G] 8.7%	*Monstrichardia aquatica* (G)
fos9	N/A	47	N/A	#N/A	**[A|A] 94.2%**	**[A|A] 92.8%**	*Nitophyllites zaisanicus* (A)

out1	N/A	130.20	N/A	[F|I] 24.3% [F|F] 18.3% [G|I] 15.9% [F|FI] 14.4% [I|I] 7.2%	[F|F] 24.3% [F|I] 23.3% [F|FI] 14.4% [G|I] 12.4% [I|I] 5.6%	[F|F] 30.8% [F|I] 24.8% [F|FI] 16.0% [G|I] 10.9%
out2	N/A	113.35	N/A	[I|I] 56.9% [I|FI] 26.2% [FI|I] 6.1%	[I|I] 49.6% [I|FI] 32.3% [FI|I] 6.6%	[I|I] 45.7% [I|FI] 39.1% [FI|I] 7.0%
out3	N/A	100.10	N/A	**[I|I] 83.7%** **[I|FI] 5.3%**	**[I|I] 83.1%** **[I|FI] 5.9%**	**[I|I] 84.7%** **[I|FI] 6.3%**
out4	N/A	92.40	N/A	**[I|I] 75.7%**	**[I|I] 75.3%** **[I|F] 5.2%**	**[I|I] 76.8%** **[I|F] 5.4%**
out5	N/A	102.90	N/A	[I|I] 63.4% [I|FI] 27.5%	[I|I] 57.0% [I|FI] 33.7%	[I|I] 52.3% [I|FI] 40.3%
out6	N/A	96.60	N/A	[I|I] 52.8% [F|I] 28.6% [A|I] 6.2% [FI|I] 5.5%	[I|I] 46.7% [F|I] 34.2% [A|I] 6.5% [FI|I] 5.8%	[I|I] 42.7% [F|I] 39.3% [FI|I] 6.4% [A|I] 5.4%
out7	N/A	86.10	N/A	**[I|I] 95.2%**	**[I|I] 95.1%**	**[I|I] 95.2%**
out8	N/A	81.30	N/A	**[I|I] 90.1%** **[E|I] 5.6%**	**[I|I] 89.6%** **[E|I] 6.1%**	**[I|I] 89.4%** **[E|I] 6.5%**
out9	N/A	76.50	N/A	**[I|I] 99.4%**	**[I|I] 99.4%**	**[I|I] 99.5%**
out10	N/A	70.35	N/A	**[I|I] 98.8%**	**[I|I] 99.0%**	**[I|I] 99.1%**
out11	N/A	68.25	N/A	**[I|I] 98.9%**	**[I|I] 99.1%**	**[I|I] 99.2%**
out12	N/A	49.35	N/A	**[I|I] 98.0%**	**[I|I] 98.2%**	**[I|I] 98.6%**

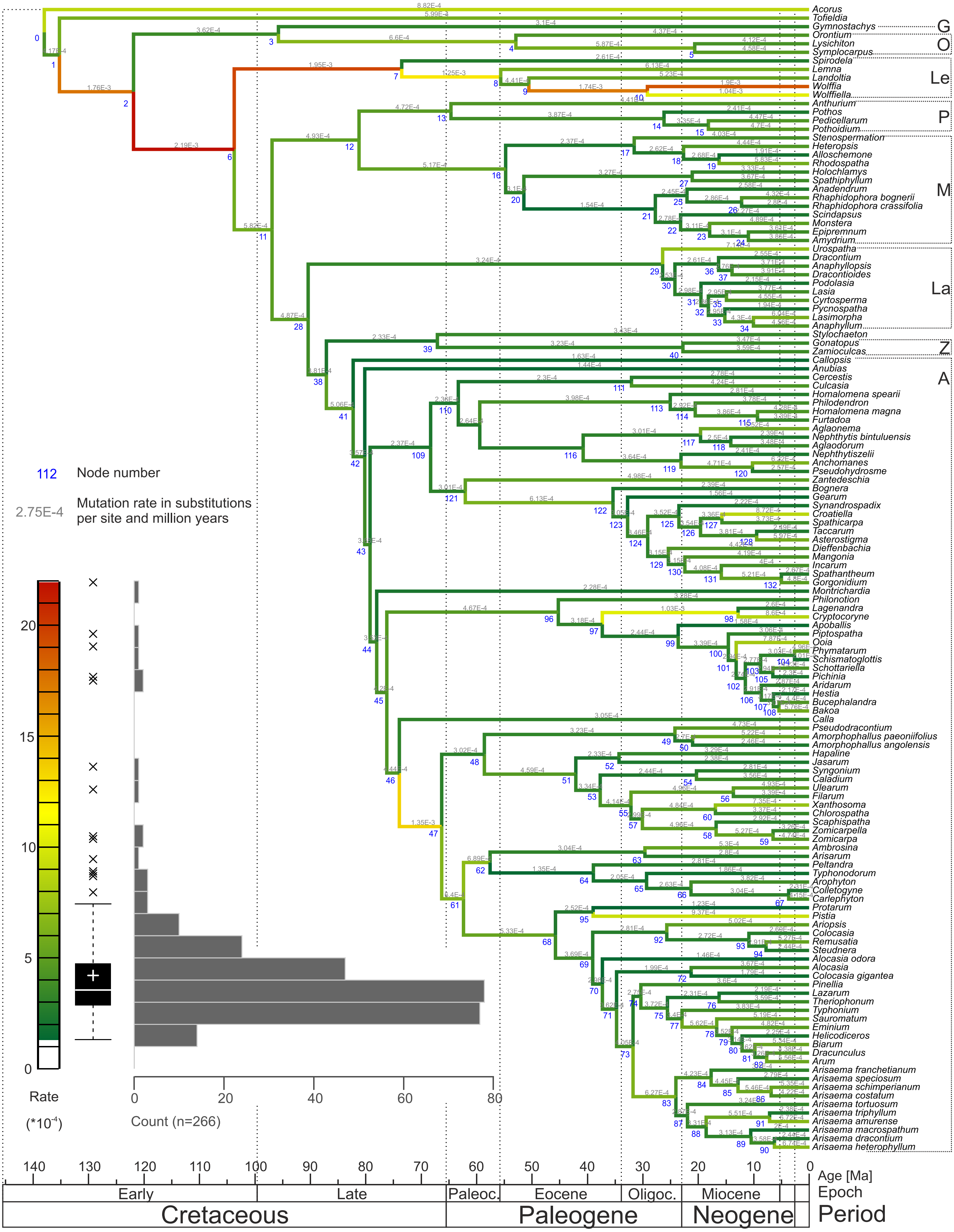


Figure S1. Inferred DNA substitution rates in the Araceae. Blue node numbers refer to nodes in Figure 3 and Table S5. Grey numbers on branches display rate in substitution per site per million years. Branches are coloured according to rate: green for low rates, yellow for medium rates, and red for high rates (see legend). The box plot graph and histogram show the distribution of substitution rates across all branches. The white line in the box plot marks the median rate, while the white cross marks the average rate. Letters in boxes next to taxon names indicate subfamilies: Gymnostachydoideae (G), Orontioideae (O), Lemnoideae (Le), Pothoideae (P), Monsteroideae (M), Lasioideae (La), Zamioculcadoideae (Z), Aroideae (A).

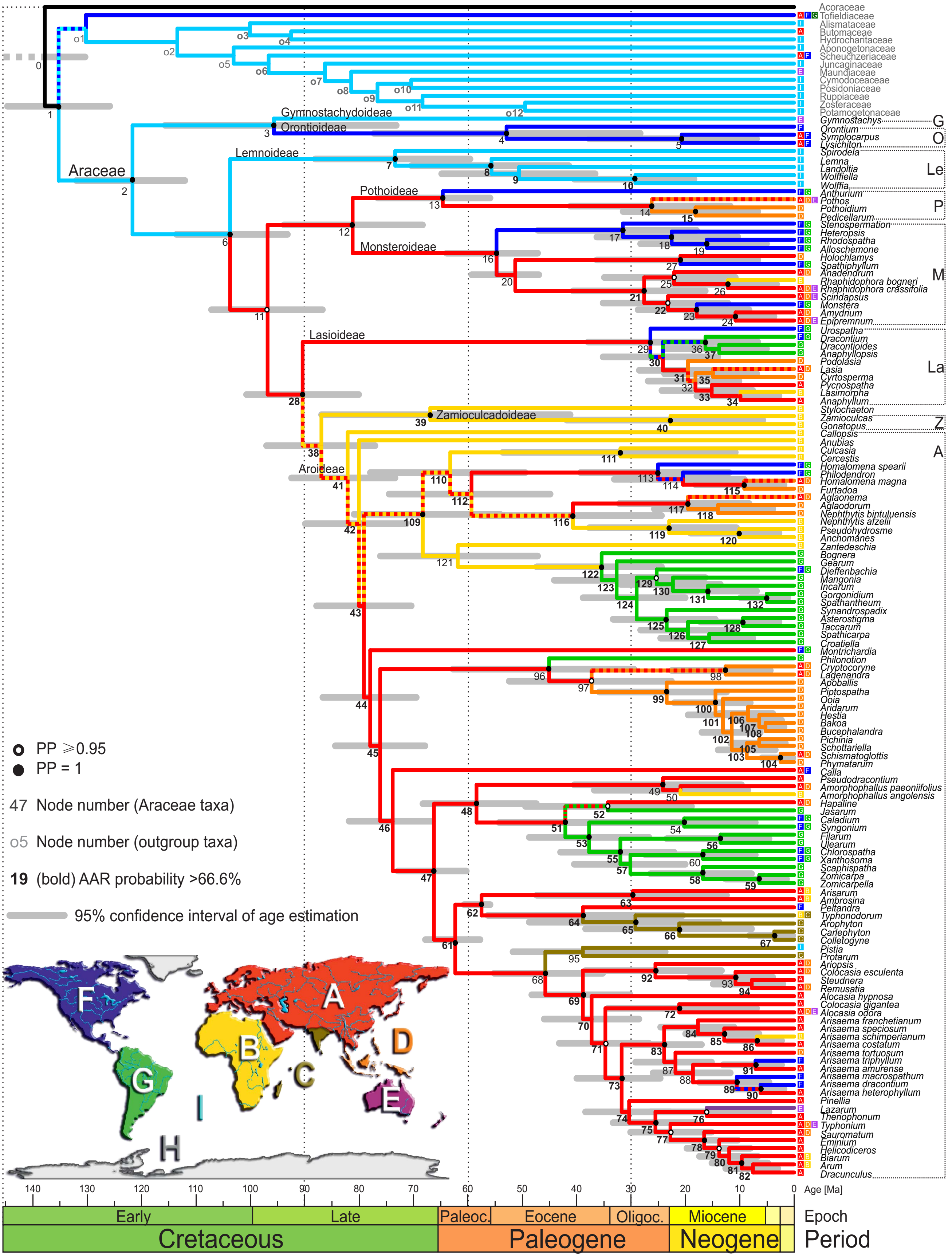
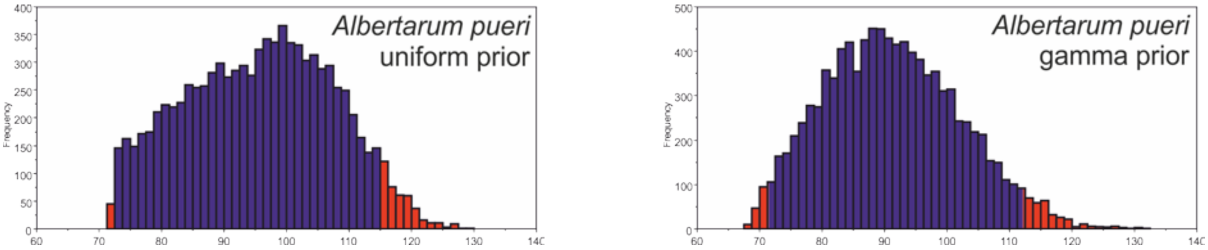
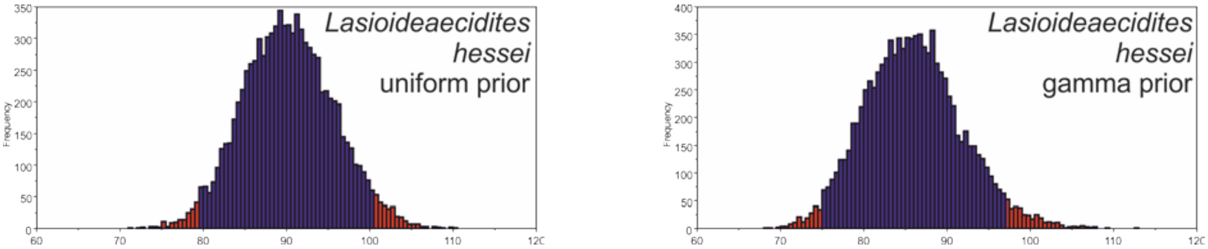


Figure S2. Results from divergence dating and ancestral area reconstruction (AAR) without fossils. Grey bars at nodes show 95% confidence intervals. Exact ages are shown in Table S5. Black dots with a white centre indicate for posterior probability (PP) of >0.95, entire black dots = 1. Araceae taxon names are in black, outgroup names in grey. Branches are coloured by area: Eurasia in red (A), Africa in yellow (B), Madagascar in ochre (C), Southeast Asia and India in orange (D), Australia in purple (E), North America in dark blue (F), South America in green (G), Antarctica grey (H), and world-wide distributed water-associated taxa in turquoise (I). Letters to the left of taxon names show the area coded for that taxon. Only the AAR with the highest probability is shown; those with bold numbers have a probability >66.6%. Letters in boxes next to taxon names indicate subfamilies: Gymnostachydoideae (G), Orontioideae (O), Lemnoideae (Le), Pothoideae (P), Monsteroideae (M), Lasioideae (La), Zamioculcadoideae (Z), Aroideae (A).

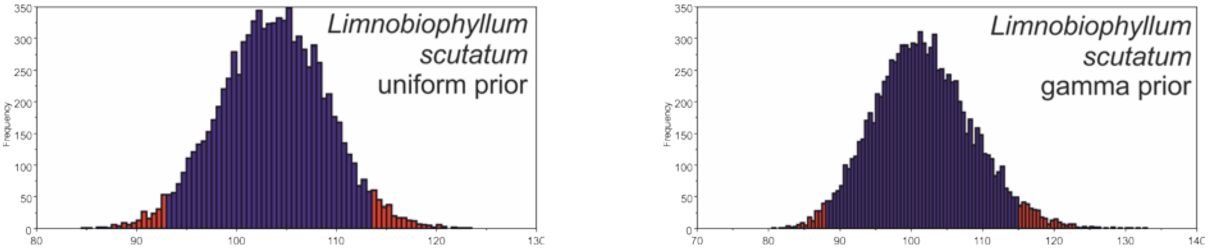
1) Orontioideae, *Albertarum pueri* (72 Ma)



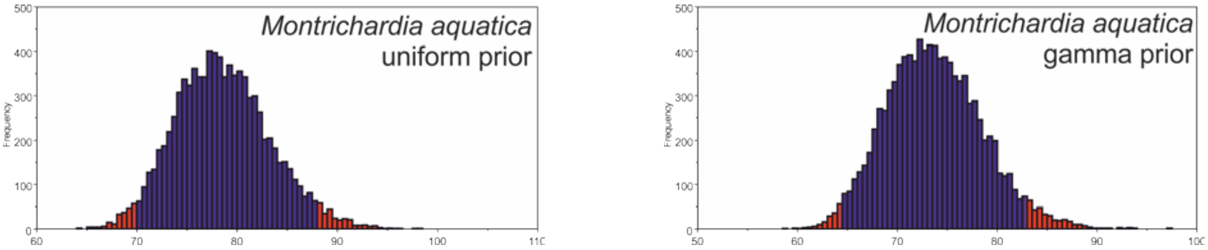
2) Lasioideae, *Lasioideaecidites hessei* (70 Ma)



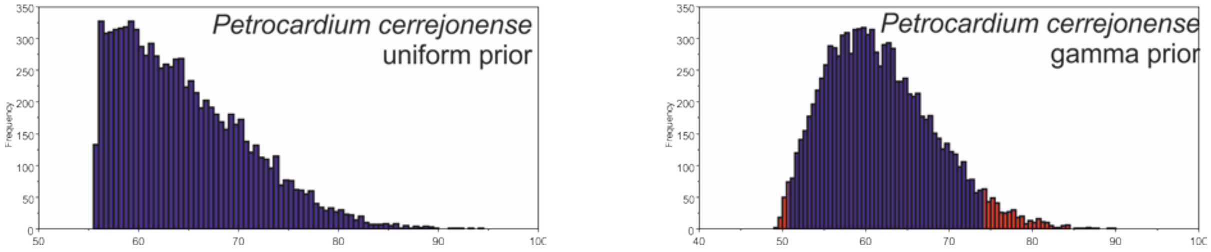
3) Lemnoideae, *Limnobiophyllum scutatum* (65.5 Ma)



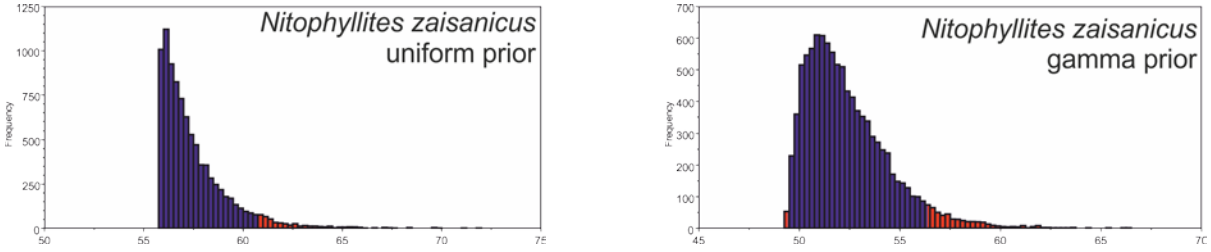
4) *Montrichardia*, *Montrichardia aquatica* (55.8 Ma)



5) *Anthurium*, *Petrocardium cerrejonense* (55.8 Ma)



6) *Typhonodorum* clade, *Nitophyllites zaisanicus* (55.8 Ma)



7) *Rhaphidophora* clade, *Araciphyllites tertiarius* (47 Ma)

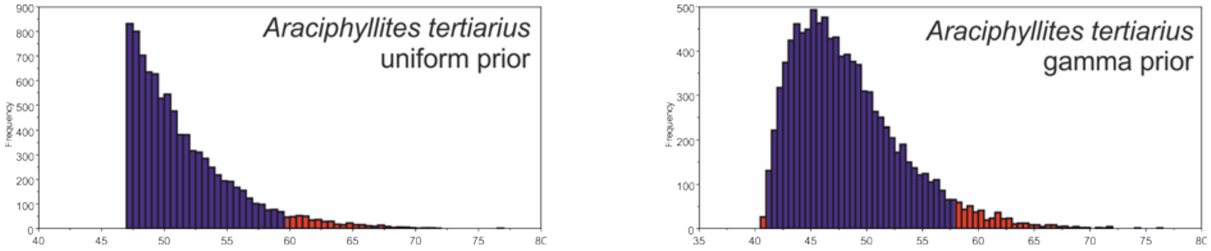


Figure S3. Posterior distribution of fossil constraints from the BEAST runs with the simple substitution model (JC + Γ) with either uniform (left column) or gamma-shaped (right column) prior distributions. The y-axis is showing the frequency, the x-axis the age in million years ago (Ma).

3

Alocasia

Giant taro and its relatives - A phylogeny of the large genus *Alocasia* (Araceae) sheds light on Miocene floristic exchange in the Malesian region

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Giant taro and its relatives: A phylogeny of the large genus *Alocasia* (Araceae) sheds light on Miocene floristic exchange in the Malesian region

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ABSTRACT

Alocasia comprises over 113 species of rainforest understorey plants in Southeast Asia, the Malesian region, and Australia. Several species, including giant taro, *Alocasia macrorrhizos*, and Chinese taro, *Alocasia cucullata*, are important food plants or ornamentals. We investigated the biogeography of this genus using plastid and nuclear DNA sequences (5200 nucleotides) from 78 accessions representing 71 species, plus 25 species representing 16 genera of the *Pistia* clade to which *Alocasia* belongs. Divergence times were inferred under strict and relaxed clock models, and ancestral areas with Bayesian and maximum likelihood approaches. *Alocasia* is monophyletic and sister to *Colocasia gigantea* from the SE Asian mainland, whereas the type species of *Colocasia* groups with *Steudnera* and *Remusatia*, requiring taxonomic realignments. Nuclear and plastid trees show topological conflict, with the nuclear tree reflecting morphological similarities, the plastid tree species' geographic proximity, suggesting chloroplast capture. The ancestor of *Alocasia* diverged from its mainland sister group c. 24 million years ago, and Borneo then played a central role in the expansion of *Alocasia*: 11–13 of 18–19 inferred dispersal events originated on Borneo. The Philippines were reached from Borneo 4–5 times in the Late Miocene and Early Pliocene, and the Asian mainland 6–7 times in the Pliocene. Domesticated giant taro originated on the Philippines, Chinese taro on the Asian mainland.

1. Introduction

The Malay Archipelago has long attracted the attention of biogeographers because of its outstanding biodiversity, endemism, and complex geological history (Wallace, 1869; Morley, 1998; Lohman et al., 2011). Of particular interest has been to understand the intermixing of ancestrally Laurasian and Gondwanan lineages in this region, and molecular phylogenies combined with molecular clocks now allow a more precise understanding of the direction and timing of such intermixing (Lohman et al., 2011; Richardson et al., 2012). Biogeographic studies of Malesian plant clades utilizing these methods are available for seven groups. These are the stone oak genus, *Lithocarpus* (Cannon and Manos, 2003), the myrmecophytic Euphorbiaceae genus *Macaranga* (Bänfer et al., 2006), the Meliaceae tribe Aglaieae (Muellner et al., 2008), the Annonaceae genus *Pseuduvaria* (Su and Saunders, 2009), the large genera *Cyrtandra* (Gesneriaceae; Clark et al., 2008) and *Begonia* (Begoniaceae; Thomas et al., 2011), and the palm genus *Livistona* (Arecaceae; Crisp et al., 2010). These studies revealed predominant west to east dispersal and diversification after the late Miocene. This general pattern may be explained by the large source region of wet forest west of the Wallace line and a later emergence of landmasses east of the Wallace line, leading to a more frequent colonization from west to east (Richardson et al., 2012).

A plant group that is extremely species-rich in the Malesian region is the Araceae, a family with a relatively extensive fossil record going back to the Upper Early Cretaceous, Paleocene, and Eocene (Friis et al., 2004, 2010; Wilde et al., 2005; Herrera et al., 2008). Among the largest genera in the family is *Alocasia*, a member of the relatively derived *Pistia* clade (Renner and Zhang, 2004; Cabrera et al., 2008; Cusimano et al., 2011). *Alocasia* currently comprises 113 species, with 27 more awaiting description (Nicolson, 1968, 1987; Hay and Wise, 1991; Hay, 1998, 1999; Boyce, 2008; PB unpublished data). The natural range of *Alocasia* extends from India and Sri Lanka through Indochina to China and southern Japan, the Malay Archipelago and Oceania; a single species is indigenous in Australia (Fig. 1). Several species are commercially important indoor plants, others are cultivated outdoors, such as *Alocasia cucullata* (Chinese taro), an ethnobotanically important plant throughout Asia, and *Alocasia macrorrhizos* (giant taro) a tropical ornamental cultivated for its tubers and leaves, used as animal fodder (Weightman, 1989; Mayo et al., 1997) . The wild origin of these two species is unknown (Hay, 1999; Boyce, 2008).

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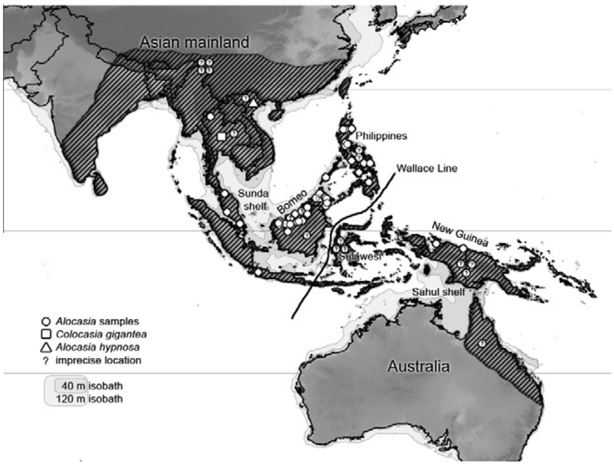

Fig. 1. Map showing the global distribution of *Alocasia* (shaded area) and origin of samples included in this study. Circles refer to *Alocasia* samples; circles with a question mark indicate locations without GPS data. The square shows the collection location of the *Colocasia gigantea* sample, the triangle that of the *Alocasia hypnosa* sample. The 40 m and 120 m isobaths are shown as pale grey outlines.

The typical *Alocasia* habitat is the understorey of perhumid lowland forest; only a few species grow >1000 m altitude or in light-gaps, clearings, or secondary vegetation (Hay and Wise, 1991; Hay, 1998; Boyce, 2008). Growth forms range from small herbaceous to thick-stemmed massive plants with huge leaves (Fig. 2). Seed dispersal is by birds and pollination by drosophilid flies (genus *Colocasiomyia*) that use the spadices as breeding sites (Ivancic et al., 2005, 2008; Sultana et al., 2006). Little is known about the specificity of *Alocasia* pollinators or hybridization in nature, but morphologically polymorphic species or species 'complexes' have been suspected as involving hybridization (Hay, 1998).

Molecularly, hybridization can be detected when plastid and nuclear sequences yield different tree topologies, which can point to the maternally inherited plastid genome coming from a different source than an individual's nuclear genome. Given the evidence for widespread hybridization and chloroplast capture in plants (Bänfer et al., 2006; Cristina Acosta and Premoli, 2010; Manen et al., 2010) it is surprising that only two studies of Southeast Asian plant groups have compared plastid and nuclear histories. In stone oaks, *Lithocarpus*, Cannon and Manos (2003) found that the nuclear DNA data contained less geographical structure than the plastid data, indicating that gene flow mediated through pollen is less restricted than purely seed-mediated (chloroplast) gene flow, and in *Macaranga*, Bänfer et al. (2006) documented plastid haplotype sharing by up to seven species and as many as six co-existing haplotypes in a single species.

Fig. 2. Representative species of *Alocasia*. Habit of *A. robusta* at disturbed forest edge, Sarawak, Malaysia (left); habit of *A. reversa* on limestone rocks, Sarawak, Malaysia (upper middle), inflorescence of *A. longiloba* '*denudata*' in rainforest understory in Singapore (right), colocasioid venation on lower leaf surface of *A. sarawakensis* in Sabah, Malaysia (lower middle).

Here we use both nuclear and plastid sequences and broad geographic sampling of species to address the following questions: (i) Is *Alocasia* monophyletic and which clade or species in the *Pistia* group is it most closely related to? (ii) Where do the cultivated species giant taro, *A. macrorrhizos*, and Chinese taro, *A. cucullata*, come from? And (iii) Do nuclear and plastid data yield congruent topologies or is there evidence of hybridization? Because of its species diversity and wide distribution range, understanding the biogeography of *Alocasia* also sheds light on floristic links across the Malesian regions.

2. Materials and methods

2.1. Taxon sampling and number of species

Of currently 113 *Alocasia* species, we here sample 71, represented by 78 plants. Table S1 provides a list of the species with author names, geographic origin of material, herbarium vouchers, and GenBank accession numbers for all sequences. Of these species, 32 were named in the past 20 years, and the discovery of new species continues (e.g., Kurniawan and Boyce, 2011). At the moment, 27 species await description once complete flowering and fruiting material is available (PB, personal collections). Our sampling covers the geographic range and morphological diversity of *Alocasia*, except for New Guinea, which is underrepresented (Hay and Wise, 1991 recognized five groups there of which our sample includes one). Of the taxonomically problematic species *Alocasia longiloba* we included 13 accessions (with nine different species names) and of *Alocasia robusta* (Fig. 2, left photo) three. Leaf material came from herbarium specimens or silica-dried leaf samples (Table S1). Determination of plant material relied on comparison with herbarium material carried out by PB and LN. As outgroups, we included 25 species representing 16 genera of the *Pistia* clade (Renner and Zhang, 2004; Cabrera et al., 2008; Cusimano et al., 2011), usually the type species of the genus name.

2.2. Isolation of DNA, amplification, and sequencing

DNA isolation followed standard protocols. To deduce phylogenetic relationships, we relied on the nuclear phytochrome C gene (*phyC*), and four plastid loci, the *trnL* intron, the *trnL-F* intergenic spacer, the *rpl20-rps12* intergenic spacer, and the *trnK*/*matK* region. Total DNA from silica-dried leaves was extracted with the NucleoSpin plant kit according to the manufacturer's protocol (Macherey–Nagel, Düren, Germany). Sequencing of the >2500 nucleotide (nt)-long *trnK* marker, amplified in one piece with the primer pair *trnK*-3914F (dicot) – *trnK*-16R (Johnson and Soltis, 1994), was problematic. Consequently, we designed new internal primers and amplified the section in four pieces: *trnK*-3914F – *trnK*-AR-alo, *trnK*-19F – *trnK*-RM-ara, *trnK*-FM-ara – *trnK*-1760R-alo, and *trnK*-1640F-alo – *trnK*-R1-mono. The new primer sequences are as follows: *trnK*-AR-alo 5′-CTC TTG AAA GAG AAG CGG ATA TAG-3′, *trnK*-19F 5′-TGT TCT GGC CAT ATC GCA CTA TG-3′, *trnK*-RM-ara 5′-AAG ATG TTG ATC GTA AAT AAG AGG-3′, *trnK*-FM-ara 5′-GTT TTG CTG TCA TTA TGG AAA TTC-3′, *trnK*-1760R-alo 5′-TAC CGC TGA AGG ATT TAT TAG GAC-3′, *trnK*-1640F-alo 5′-GGG ACT CAT CTT

CTG ATG AAG AAA-3′, *trnK*-R1-mono 5′-CAT TTT TCA TTG CAC ACG RC-3′. *PhyC* was also amplified in two pieces with the newly designed primers: A20F – 748R and 430F – AR: A20F: 5′-CAC TCA ATC CTA CAA ACT GGC-3′, 748R: 5′-ACA AGA TCC ATG ACA TTA GGT GAT T-3′, 430F: 5′ CTC GTG ATG TCT GTC ACA ATA AG-3′ and AR: 5′-GAA TAG CAT CCA TTT CAA CAT C-3′. The *rpl20–rps12* intergenic spacer was amplified using the primers and PCR conditions described in Renner and Zhang (2004). The *trnL* intron and *trnL*-F intergenic spacer was amplified according to Taberlet et al. (1991) with the primer pairs c–d and e–f, respectively. PCR products were cleaned using the NucleoSpin® Extract II kit (Macherey–Nagel, Dueren, Germany), and sequencing reactions were run on an ABI 3130 capillary sequencer (Applied Biosystems), following the manufacturers' protocols. Sequence editing and alignment were carried out in Sequencher 4.7 (Gene Codes, Ann Arbor, Michigan, USA) and McClade 4.0 (Maddison and Maddison, 2000). New sequences generated for this study have been deposited in GenBank (accession numbers in Table S1), and alignments for this study in TreeBASE (submission ID 12182).

2.3. Phylogenetic analysis

Individual and combined phylogenetic analyses were performed under likelihood (ML) optimization and the GTR + Γ substitution model, using RAxML 7.0.4 (Stamatakis, 2006) and the RAxML-GUI 0.93 (Silvestro and Michalak, 2010). Statistical support was assessed via 100 bootstrap replicates. Throughout this paper, 70–84% bootstrap support is considered moderate and 85–100% strong support.

2.4. Divergence dating

Dating relied on Bayesian divergence time estimation as implemented in BEAST 1.61 (Drummond et al., 2006; Drummond and Rambaut, 2007). Identical sequences and sequences differing only in nucleotide ambiguities were removed, yielding a matrix of 81 species (56 *Alocasia*). For the dating runs, we used the HKY + Γ model of substitution, which is an extension of the K80 + Γ model identified as the best fit in jModelTest (Posada, 2008), and a Yule tree prior as the tree model. Runs were repeated under either a strict clock model or a relaxed clock model, the latter with rate variation across branches uncorrelated and lognormally distributed. MCMC chains were run for 16 million in the strict clock model, and for 50 million generations in the relaxed clock model, with parameters sampled every 1600th and 5000th generation, respectively. Tracer (1.50) was used to assess effective sample sizes (ESS) for all estimated parameters and to judge the percentage of burn-in for tree constructions. Trees were combined in TreeAnnotator (1.6.1), and maximum clade credibility trees with mean node heights were visualized in R (www.r-project.org) with the package phyloch (www.christophheibl.de/Rpackages.html).

For calibration, we used the age of the leaf fossil *Caladiosoma messelense* from the Messel Formation near Frankfurt, Germany (47–47.5 Ma), which resembles species of *Alocasia* and *Colocasia* in its colocasioid leaf venation (Fig. 2). This venation consists of fine veins that branch almost at right angles from the primary lateral veins and arch towards the leaf margin, sometimes fusing to an interprimary collective vein. It occurs in *Alocasia*, *Colocasia*, *Ariopsis*, *Remusatia*, and *Steudnera*, but also in the South American genera *Caladium* and *Xanthosoma*. The Eurasian origin of the fossil, however, fits better with a placement as a relative of Southeast Asian Araceae. Other members of the *Pistia* clade, such as the Areae, do not possess colocasioid venation, either due to a loss of the character or because of multiple gains in *Alocasia*, and the *Colocasia* clade. To account for the uncertain placement of *C. messelense* in the *Pistia* clade, we explored the effects of different *fossil-cum-topology* combinations on the resulting age estimates (*Results*), always using a normally distributed prior age distribution that had a mean of 47.25 Ma and a standard deviation (SD) of 0.15 Ma. This narrow SD is justified by the well-constrained dating of the Messel Formation (V. Wilde, Senkenberg Museum, Frankfurt, Germany, pers. comm., 2009). Additionally, one run was performed without constraining the topology. We also ran an analysis with an empty alignment (the "prior-only" option in BEAST) to compare the posterior parameter values without and with the data. This allows evaluating the influence of prior distributions on the outcome of Bayesian analyses. For absolute ages we relied on the geologic time scale of Walker et al. (2009).

2.5. Ancestral area optimization

To infer the geographic history of *Alocasia*, we used two approaches: Dispersal vicariance analysis (DIVA) in a Bayesian framework, using the S-DIVA (Statistical Dispersal-Vicariance) program in RASP 1.1 (Yu et al., 2010, 2011), and a dispersal-extinction-cladogenesis model (DEC) in a likelihood framework, using Lagrange (Ree et al., 2005; Ree and Smith, 2008). S-DIVA applies the DIVA method of Ronquist (1997) to the multiple trees from a Bayesian analysis, which has the advantage that uncertainties in phylogenetic inference can be taken into account. In contrast, Lagrange uses a likelihood approach that takes into count the branch length of a given tree. As input for S-DIVA we used the BEAST MCMC tree chain obtained under the strict clock model applied to the nuclear data (minus the burn-in of the divergence dating analysis) and the maximum clade credibility tree to plot the results. As input tree for Lagrange we used the same BEAST maximum clade credibility tree. A Python script was created using the online Lagrange configurator. We did not constrain the dispersal probabilities to avoid over-parameterization.

Species distributions were categorized into eight areas: (A) Asian mainland (including Sumatra and Java), (B) Borneo (including the Philippine island Palawan, which geologically belongs to the Sunda shelf), (C) The Philippines, (D) Sulawesi, (E) New Guinea, (F) Australia, (G) Mediterranean area, and (H) Seychelles. In S-DIVA, as combined ancestral areas we allowed three combinations: Asia with the Mediterranean area (AG), the Asian mainland with Borneo (AB), and New Guinea with Australia (EF). Lagrange requires connectivity between areas, which we provided by allowing combined ancestral areas of adjacent regions: AB, AG, AH, BC, BD, CD, CE, DE, and EF. *Alocasia* spec. nov. BO07, from the Botanical Garden in Bogor has identical nuclear sequences as *Alocasia portei* and *A. macrorrhizos*. Its reported origin (Sulawesi) could not be verified, and it was therefore excluded from this analysis.

3. Results

3.1. Sequence data

Four hundred twenty-one sequences were newly generated for this study. The aligned *trnL* sequences comprised 731 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 808 nucleotides of which we excluded 22 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 entirety for a length of 2504 aligned positions. The alignment of the nuclear low copy gene *phyC* comprised 1074 nucleotides, including four that showed double peaks. These sites were excluded from phylogenetic analyses.

3.2. Phylogenetic relationships in the plastid and nuclear trees

Plastid trees from the four data partitions revealed no statistically supported discrepancies and the sequences were therefore concatenated. Comparison of the combined plastid tree with the nuclear *phyC* tree, however, revealed topological contradictions. In both trees, species of *Alocasia* form a strongly supported clade with the exception of *Alocasia hypnosa*, which in the plastid tree (Fig. 3a) is sister to most of the remaining *Pistia* clade, but in the nuclear tree is placed more centrally in the *Pistia* clade (Fig. 3b). For the remaining taxa, both trees reveal the same main lineages: (a) *Alocasia* plus *Colocasia gigantea* (indicated by yellow branches in Fig. 3), (b) the Areae clade (*Arisaema*, *Arum*, *Biarum*, *Dracunculus*, *Eminium*, *Helicodiceros*, *Lazarum*, *Pinellia*, *Sauromatum*, *Theriophonum*, *and Typhonium*; blue branches in Fig. 3), and (c) the *Colocasia* clade (*Colocasia* as to its type species, *Ariopsis*, *Remusatia*, and *Steudnera*; green branches in Fig. 3).

Within core *Alocasia* (excluding *A. hypnosa*), the plastid phylogeny shows six geographic clades, numbered and color-coded in Fig. 3a. An Asian mainland clade (clade i shown in green) is sister to a polytomy that comprises a Philippine clade (clade ii shown in purple), a New Guinean clade (iii, yellow), a Bornean clade (iv, blue), another Asian mainland clade (v, green), and a poorly supported clade of Bornean and Philippine species (vi, blue). The position of the sole Australian species of *Alocasia*, *A. brisbanensis*, remains unresolved.

The nuclear phylogeny revealed four main clades (labeled A to D in Fig. 3b), which often include species with similar morphological traits. Clade A contains most species of the *longiloba* group. All have strongly rhythmic growth, thinly membranous cataphylls, and solitary or rather few leaves with often peltate, pendulous blades; however, two Sulawesian species that morphologically are convincingly part of this group are in Clade C. Clade A further contains a group of massive species with syleptic renewal, bi-modular inflorescences, long petiolar sheath, and large, short-lived leaves that all occur in the Indochinese region. Clade B comprises all species with a massive caulescent habit, including species with proleptic renewal growth (e.g., *A. robusta*) and sylleptic renewal growth (e.g., *A. macrorrhizos*). Clade B also includes the edible *A. macrorrhizos* and three accessions of *A. robusta*. Clade C contains only species with short-lived leaves and proportionately long petiolar sheaths, including the New Guinean *Xenophya* species group (Nicolson, 1968), which has hemianatropous or anatropous ovules and a usually persisting spathe limb (Hay and Wise, 1991). Clade D contains small or robust often lithophytic species usually referred to as the *princeps* group (*Alocasia princeps*, *Alocasia pangeran*, *Alocasia principiculus*, *Alocasia wongii*, *Alocasia ridleyi*, *Alocasia "inopinata"* (P. Boyce, ined.), and *Alocasia reversa*), characterized by long erect petioles, narrowly triangular leaf blades, the lower spathe constriction occurring well above the sterile interstice between the pistillate and staminate flowers, relatively elongated inflorescences with tapering appendices (Hay, 1998), and the similar *scabriuscula* group (*Alocasia scabriuscula*, *Alocasia melo*, *Alocasia reginula*, *Alocasia kulat*, *Alocasia reginae*, *Alocasia chaii*, *Alocasia infernalis*, and *Alocasia nebula*), characterized by leathery to subsucculent leaves, several to many inflorescences not interspersed by foliage leaves, and the spathe constriction often above the sterile interstice of the spadix (Hay, 1998).

Topological differences between the plastid and nuclear trees were also found in the taxonomically problematic *A. robusta* and *A. longiloba* of which our sampling included, respectively, three and 13 accessions (the last with nine species names). In the nuclear tree, 11 of the 13 accessions of the *A. longiloba* species complex group together (yellow bar in Fig. 3b), while in the plastid tree (3a) they are partly found in clade I, partly in clade iv, and partly in clade v. The three accessions of *A. robusta* group together in the nuclear tree (clade B in Fig. 3b), although the *phyC* sequences of the two Sabah plants differ from the Sarawak plant in two substitutions. In the plastid tree (Fig. 3a), the Sabah plants have identical sequences, but the plant from Sarawak differs substantially.

3.3. Divergence time estimation

Divergence time estimation (Fig. 4) relied on the nuclear dataset because it better reflects bi-parental inheritance. Since the relationships of *A. hypnosa* to the other groups (*Alocasia*/*C. gigantea*; the *Colocasia* clade; and the Areae clade; color-coded in Fig. 3) were not confidently resolved by our data, calibration with the *Caladiosoma messelense* leaf fossil (Section 2) was applied to 15 possible topologies for these clades. The results (Table S2) show that ages in the *Alocasia* crown node hardly differed among the 15 trees. The best ESS values were reached with the topology in which the Areae were sister to the remaining taxa, and the topology obtained from an unconstrained run also showed this placement of the Areae. The strict clock model and the relaxed clock model gave estimates for the *Alocasia* crown that on average differed by 6.16 ± 0.9 Ma, with the relaxed clock model yielding older ages. Mean ages from the strict clock model generally fall inside the 95% highest posterior density (HPD) intervals of the relaxed model, but the converse is not the case (Table S2). The mean *phyC* substitution rate was 0.00060 ± 0.00001 per site/million years under the strict clock and 0.000055 ± 0.00003 under the relaxed clock.

According to the strict clock model, the split between *Alocasia* and *C. gigantea* occurred at 24.1 Ma, i.e., the transition of the Oligocene to the Miocene, and *Alocasia* began diversifying in the Mid-Miocene (13.5 Ma). Dates are ~1.47 times older in the relaxed clock analysis, which places the stem of *Alocasia* in the Mid-Oligocene (29.1 Ma) and its crown in the Early Miocene (19.3 Ma). Exact dates with HPD for biogeographically important nodes are shown in Table S2, and for all nodes in the preferred tree in Table S3.

3.4. Ancestral area optimization

Bayesian (S-DIVA) and likelihood-based (Lagrange) ancestral area reconstruction on the nuclear tree yielded mostly congruent ancestral areas except for nodes 24, 26, and 41 (marked in bold in Fig. 4 and Table S3). Node 24 involves the sparsely sampled outgroups *Sauromatum* and *Lazarum*. Nodes 26 and 41 are the deepest splits in core *Alocasia* (i.e., excluding *A. hypnosa*, which clearly is not a member of a monophyletic genus *Alocasia*). S-DIVA and DEC both inferred that the split between *Alocasia* and *C. gigantea* occurred on the Asian mainland, but they differed in the inferred distribution of most recent common ancestor of the *Alocasia* crown group (node 26): S-DIVA inferred an origin in Asia, Lagrange an origin on Borneo. Both approaches inferred the combined area Sundaland as the second-most probable ancestral region for this node. For node 41, Lagrange inferred an origin on Borneo, while S-DIVA inferred an origin on the Asian mainland. S-DIVA also inferred combined ancestral areas more often than did Lagrange, resulting in the inference of fewer dispersal events by S-DIVA. Of the 54 divergence events in the tree, 18 or 19 involve dispersal events, with the majority dispersals out of Borneo (13 inferred by Lagrange, 11 by S-DIVA), in contrast to only three or four dispersal into Borneo. The Philippines were colonized 4–5 times and are the likely region from which New Guinea and Australia were colonized (node 42 in Fig. 4). Sulawesi was reached once from Borneo and once from the Philippines. Dispersal and divergence events are more or less evenly distributed over time (Fig. 4).

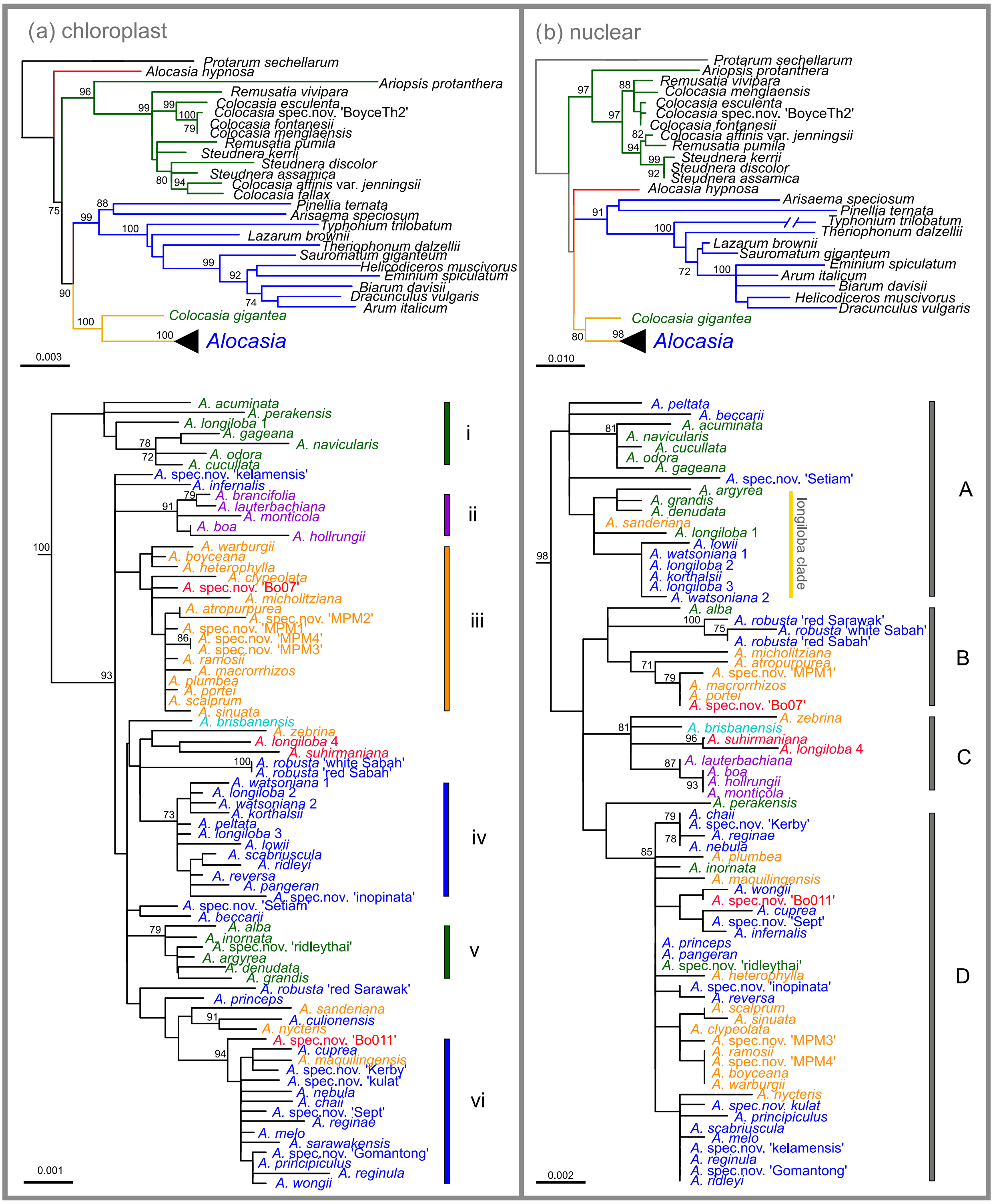

Fig. 3. Maximum likelihood (ML) phylogenies for *Alocasia* and its outgroups obtained from the plastid DNA data (a) and nuclear DNA data (b). The upper section of each tree shows the outgroups, the lower section the ingroup. Numbers at nodes indicate ML bootstrap support from 100 replicates. Species names are colored according to the origin of the samples; green: Asian mainland, blue: Borneo, orange: Philippines, red: Sulawesi, purple: New Guinea, cyan: Australia. Branch colors indicate the main clades among the outgroups; green: *Colocasia* clade, blue: *Areae* clade, red: *Alocasia hypnosa*. Clades discussed in the text are marked by letters.

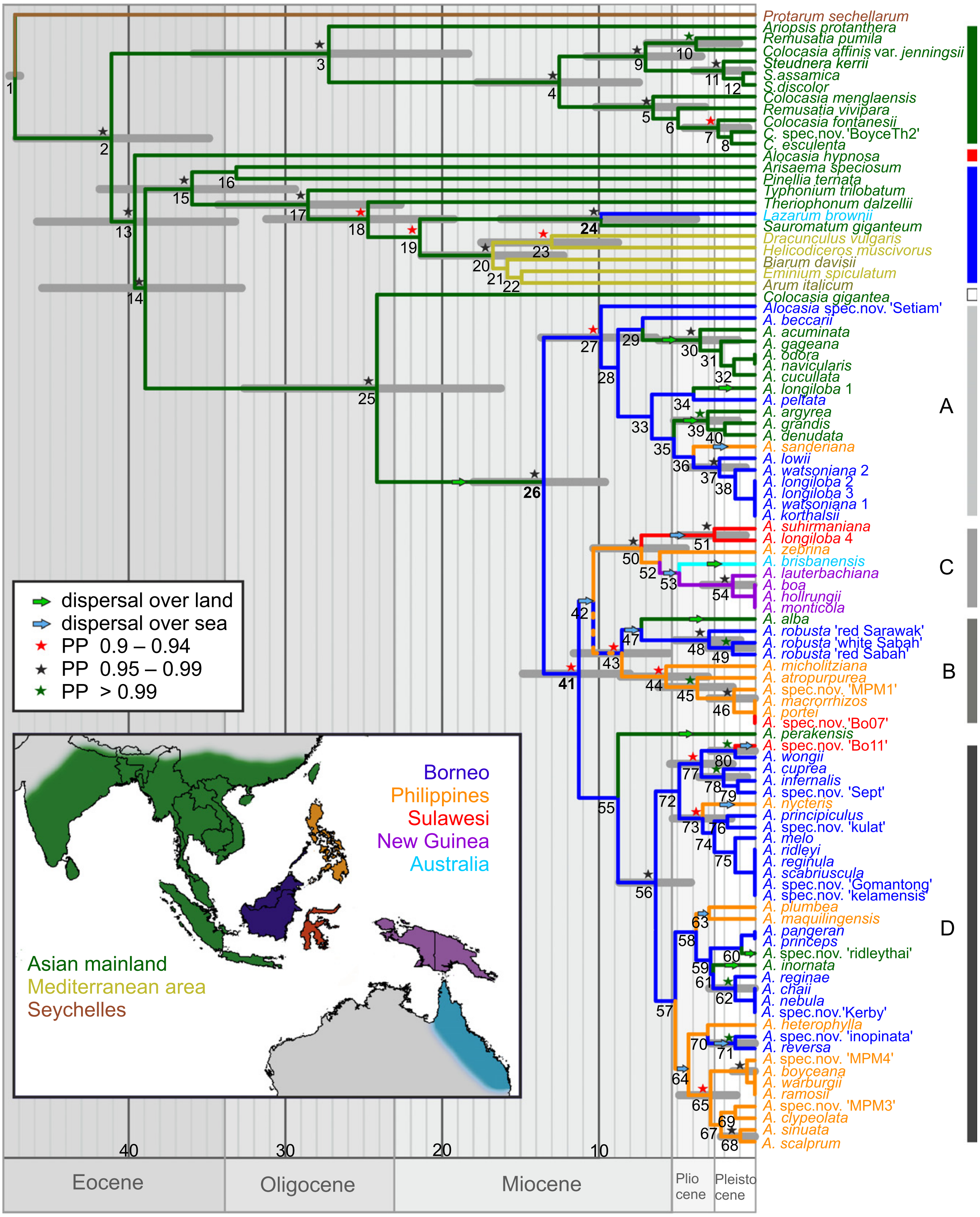

Fig. 4. Chronogram for *Alocasia* and its outgroups obtained from nuclear DNA data modeled under a global clock. Node heights represent mean ages and bars the 95% highest posterior density intervals. Species names are colored according to the geographic origin of the sample, with branch colors indicating the most likely area inferred with the DEC approach. Green arrows indicate dispersal over land and blue arrows over sea. Ancestral areas at nodes 24, 26, and 41 (in bold) were reconstructed differently in S-DIVA and DEC. Stars at nodes indicate levels of support; black: PP > 0.99, green PP > 0.95, red: PP > 0.9. Divergence times and posterior probability values for each node are listed in Table S3. Clades discussed in the text are marked by letters. An asterisk (*) marks accessions with near-identical sequences, that were excluded from dating analyses.

4. Discussion

4.1. Monophyly and phylogenetic relationships

The least expected findings of this study probably are that a monophyletic circumscription of *Alocasia* requires the removal of *A. hypnosa* and that the closest relative of *Alocasia* is *Colocasia gigantea*, while the type species of *Colocasia* (*C. esculenta*) groups elsewhere in the phylogeny of the *Pistia* clade (Fig. 3). *Colocasia gigantea* occurs naturally from Southwest China, Indochina, and Thailand through Peninsular Malaysia and Sumatra to Java. This large-flowered species was originally described as *Caladium giganteum* (Blume, 1823), and Schott (1857) then made it the basis of a new genus, *Leucocasia*, recognizing that it did not fit in *Caladium* because of its unilocular ovaries with sub-orthotropous ovules. Later, Hooker (1893) transferred the species to *Colocasia* where it indeed fit well in terms of its placentation and leaf thickness. A few species of *Alocasia*, for example, *A. macrorrhizos*, however, also have such leaves. Since the name *Colocasia* must stay with *C. esculenta*, *C. gigantea* could now either be reinstated as *Leucocasia gigantea* (as yet another monospecific genus of the Araceae) or it could be transferred into *Alocasia*.

Alocasia hypnosa, the surprising non-*Alocasia* discovered here, was described in 2005 from plants collected in southern Yunnan, China, and then cultivated at the Xishuangbanna Botanical Garden (Wang et al., 2005). It has recently also been collected in northern Vietnam. The species is characterized by a purple spathe, numerous long stolons, and seasonal deciduousness and was placed in *Alocasia* because of its few basal ovules, red colored fruits, and its overall similarity to *Alocasia odora*. Our data reveal that it is a genetically highly distinct lineage of the *Pistia* clade, but more loci will need to be sequenced for a secure placement of this species.

4.2. Incongruence of nuclear and plastid phylogenies, and relationships in the A. robusta and A. longiloba species groups

Most *Alocasia* clades in the plastid phylogeny (Fig. 3a) are restricted to a particular geographic region. By contrast, most major clades in the nuclear phylogeny comprise morphologically similar species from the Philippines, Asia, and Borneo (Fig. 3b). The morphological similarities were specified in section 3.2 and mainly concern species of the *longiloba* group, the *scabriuscula* group, the *princeps* group, and the *Xenophya* group (Nicolson, 1968; Hay and Wise, 1991; Hay, 1998).

The observation that relationships seen in plastid data, which reflect maternal inheritance (and local seed dispersal), correlate with geographic proximity, while those seen in nuclear data correlate more with morphological species boundaries has been made in many other studies (e.g., Soltis and Kuzoff, 1995; Cristina Acosta and Premoli, 2010; Manen et al., 2010; Rautenberg et al., 2010). For South-East Asia, this is the case in stone oaks (Cannon and Manos, 2003) and *Macaranga* (Bänfer et al., 2006). Where plant species hybridize (even just occasionally), the combination of mostly local seed dispersal and obligate out-breeding (via interplant pollen transport) may lead to the long persistence of the genetic signal left by the hybridization. Such conditions would seem to apply in *Alocasia*, in which complete temporal separation of individuals' male and female function enforces outcrossing and in which seed dispersal is by understory birds. The *Colocasiomyia* flies that pollinate *Alocasia* sometimes visit co-flowering *Alocasia* species although it is not known whether they can successfully oviposit in more than one species (Toda and Lakim, 2011). Many cultivated species of *Alocasia* have been crossed, including phylogenetically distant ones (Garner, 2010; L. Garner, Aroidea research, Florida City, Florida, pers. comm., February 2011; *A. odora* × *A. nycteris*, *A. odora* × *A. portei*, *A. macrorrhizos* × *A. sinuata*), suggesting that hybridization may also occur in nature.

The morphologically polymorphic species *A. robusta* and *A. longiloba* of which we included several accessions both revealed nuclear/plastid tree discrepancies. The accessions of *A. robusta* from Sabah and Sarawak group together in the nuclear tree (Fig. 3b; clade B), even though *phyC* sequences of the two Sabah plants differ from the Sarawak plant in two substitutions. In the plastid tree (Fig. 3a), the Sabah plants have identical sequences, but the plant from Sarawak differs substantially and placed apart from the other two. Typical *A. robusta* (Fig. 2, left photo) has dark red spathe limbs, and mature inflorescences that smell of decomposing meat, suggesting sapromyophilous pollination. A form with white spathe limbs and sweet odor exists in Sabah, where it co-occurs with the red spathe form (Hay, 1998), and our two accessions represented these color morphs.

The *A. longiloba* species complex comprises seven species from Sundaland und Sulawesi that share unifoliar growth modules and a non-persistent lower spathe during fruit ripening, viz. *Alocasia denudata*, *Alocasia korthalsii*, *A. longiloba*, *Alocasia lowii*, *Alocasia putzeysii*, *Alocasia thibautiana*, and *Alocasia watsoniana* (Hay, 1998; our Fig. 3). Hay saw them as closely related to *Alocasia sanderiana* (Philippines), *Alocasia boyceana* (Philippines), and *Alocasia suhirmaniana* (Sulawesi). We sampled all these species except *A. putzeysii* and *A. thibautiana*. The nuclear phylogeny (Fig. 3b) shows that the *longiloba* group sensu Hay indeed clusters with *A. sanderiana* as he suggested, but also with *Alocasia grandis* and *Alocasia agyrea*, which he did not consider part of the *longiloba* complex. The estimated divergence dates of the relevant species fall in the Pliocene (Fig. 4) and are thus relatively old. *Alocasia lowii* from Borneo is distinguished by two substitutions in its nuclear *phyC*-gene from *A. watsoniana* and *A. korthalsii*, perhaps reflecting beginning speciation. In Sarawak, *A. lowii* is restricted to limestone hills, where *A. korthalsii* and *A. watsoniana* have never been found.

4.3. Divergence date estimation and the role of dispersal in Alocasia

The inferred stem age of *Alocasia* and other ages inside the genus are robust to topological changes in the *Pistia* clade (Table S2). In the following discussion, we focus on the *Alocasia* ages obtained under the strict clock model, which on average were younger than those obtained with the relaxed clock. We prefer this model because it uses fewer parameters than the relaxed clock model, reducing the risk of over-parameterization. Diversification in *Alocasia* apparently began in the Middle Miocene and intensified in the Late Miocene and Pliocene (Fig. 4). Spread from the Asian mainland to the Malesian region can be inferred from the distribution of the relevant outgroups, including the closest living relative of *Alocasia*, *Colocasia gigantea* (Fig. 1).

Borneo has played a central role in the geographic expansion of *Alocasia*. Although only reached 3–4 times, 11–13 of the 18–19 inferred dispersal events originated on Borneo. The Philippines were reached from Borneo 4–5 times in the Late Miocene and Early Pliocene, and the Asian mainland was "recolonized" 6–7 times in the Pliocene. Even though Borneo is the clear center of *Alocasia* dispersal in the Sunda region, the eastern part of the Malesian Archipelago was colonized from the Philippines. At least one dispersal event occurred from the Philippines to Sulawesi in the late Miocene and a second to New Guinea and Australia at the Miocene/Pliocene boundary, followed by a single recent dispersal from Borneo to Sulawesi. The west to east dispersal of *Alocasia* with several crossings of the Wallace line started at approximately 5–7 Ma as also found in Aglaieae (Muellner et al., 2008), *Pseuduvaria* (Su and Saunders, 2009), and *Begonia* (Thomas et al., 2011). Overall, we inferred at least 10 dispersal events across ocean expanses (light-blue arrows in Fig. 4). *Alocasia* fruits are red berries, 0.3–1 cm in diameter and dispersed by understory birds, but we know of no field observations on the ecology of dispersal, germination, and seedling establishment. The closest living relative revealed in this study, *Colocasia gigantea*, produces white fruits that measure only 5 mm in diameter and are densely packed along an infructescence.

New Guinea is the only region underrepresented in our sampling (Hay and Wise, 1991; cf. Section 2.1). The five New Guinean species included here belong to a morphologically homogeneous group, called *Xenophya* group (Nicolson, 1968). Of the eight unsampled New Guinean species, two belong to the *Xenophya* group and six do not (Hay and Wise, 1991). This suggests that New Guinean *Alocasia* may comprise more independent arrivals than just the one inferred here.

Overall the inferred node ages match the tectonic and climate history of the Malesian region. Collision between the Australian and Eurasian plates started in the Late Oligocene, about 25 Ma ago (Hall, 2002, 2009) and led to island emergence. Mid-Miocene pollen records indicate a warm, moist climate and rainforest expansion on these newly forming islands (Morley, 1998), and groups adapted to rainforest understorey, such as *Alocasia*, could therefore plausibly spread and diversify. Land bridges repeatedly connected some areas, including New Guinea and Australia on the Sahul shelf, and Indochina, Sumatra, Java, and Borneo on the Sunda shelf. During the last glacial maximum (LGM), sea levels were approximately 120 m lower than today, resulting in the complete exposure of the Sunda shelf and allowing overland migration between the Asian mainland and Borneo, and even sea level reduction by just 40 m already connected these islands (Fig. 1, 40 m isobath). Such sea level lowering occurred several times, mainly in the Pleistocene, but probably also during the Pliocene and the late Miocene (Miller et al., 2005). Whether *Alocasia* could take advantage of such newly exposed land bridges would have depended on the new biota; savanna vegetation during the LGM on much of the exposed shelf area (as suggested by Bird et al., 2005 and Cannon et al., 2009) would have hindered migration of rainforest-associated *Alocasia* species. Indeed, of the 24 *Alocasia* lineage splits that fall into the Pleistocene (Fig. 4), only one involves a range expansion on the Sunda shelf (from Borneo to Asia).

4.4. Geographic origin of the cultivated species A. cucullata and A. macrorrhizos

The ornamental *Alocasia cucullata* (Chinese taro) and the tuber crop *A. macrorrhizos* (giant taro) have been cultivated for a long time (Boyce, 2008). Starch grains of *A. macrorrhizos* have been found on Solomon Island stone tools dated to 27,000 years before present (Loy et al., 1992). Today, *A. cucullata* is found in gardens throughout tropical Asia, and *A. macrorrhizos* throughout the tropics. Neither species has been found far from human settlements (Hay, 1999; Boyce, 2008). Our plastid and nuclear trees place *A. cucullata* close to *A. odora* and *Alocasia navicularis* inside an Asian mainland clade (Fig. 3a and b). The inferred recent divergence of these three species (1.31 Ma, 0–2.9 95% HPD; Fig. 4) and their low sequence divergence (6 substitutions in plastid sequences of *A. cucullata* compared to *A. odora*, 11 to *A. navicularis* and one in the nuclear sequences) point to *A. cucullata* being a domesticated form of *A. odora* or *A. navicularis*, which both range from India through Indochina to South China.

Alocasia macrorrhizos groups with Philippine species and is identical in its nuclear sequences with *A. portei* and a plant of unknown origin cultivated in the Bogor Botanical Garden (*Alocasia* spec. nov. Bo7). Hay (1998) already suspected a Philippine origin of *A. macrorrhizos* and suggested hybridization with *A. portei*.

5. Conclusions

The diversification of *Alocasia* started in the Miocene (at c. 13.5 Ma under a strict clock model or c. 19.3 Ma under a relaxed clock), when the climate changed to warm and humid conditions, which led to the expansion of rainforest in the Malesian region. Exposed land bridges and smaller inter-island distances due to lower sea levels permitted repeated clade expansion from and to Borneo and the Philippines, as well as occasional crossing of the Wallace line to Sulawesi, New Guinea, and Australia. That the plastid tree topology reflects geographic proximity while the nuclear tree more closely matches morphological resemblance, suggests occasional hybridization and local seed dispersal (reflected in the maternal plastid tree) as documented in many other plant genera (Soltis and Kuzoff, 1995; Cannon and Manos, 2003; Bänfer et al., 2006; Cristina Acosta and Premoli, 2010; Manen et al., 2010; Rautenberg et al., 2010). Giant taro, *A. macrorrhizos*, which is now cultivated in gardens worldwide, originated on the Philippines, while the Chinese taro, *A. cucullata*, originated on the Asian mainland. More generally, our findings underline the great mobility of plants, the increased recognition of which from dated molecular phylogenies is among the main paradigm shifts in the field of biogeography in recent years.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2011.12.011.

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Table S1. Species of Araceae included in this study with their author names, geographic origin of material, herbarium vouchers, and GenBank accession numbers for all sequences.

Name	**Voucher**	**trnL**	**trnLF**	**trnK / matK**	**rpl20-rps12**	**phyC**
Alocasia acuminata Schott	P. Boyce s.n. (QSBG)	JQ238645	JQ238727	JQ238813	JQ238900	JQ083496
Alocasia alba Schott	NSW 4171562	JQ238646	JQ238728	JQ238814	JQ238901	JQ083497
Alocasia argyrea Sander	BG Munich V1398	JQ238647	JQ238729	JQ238815	JQ238902	JQ083498
Alocasia atropurpurea Engl.	M. Medecilo 463 (De La Salle University Dasmariñas Herbarium)	JQ238648	JQ238730	JQ238816	JQ238903	JQ083499
Alocasia beccarii Engl.	P. Boyce AL-194 (SAR)	JQ238649	JQ238731	JQ238817	JQ238904	JQ083500
Alocasia boa A. Hay	J. Bogner 2621 (M)	JQ238650	JQ238732	JQ238818	JQ238905	JQ083501
Alocasia boyceana A. Hay	M. Medecilo 471 (De La Salle University Dasmariñas Herbarium)	JQ238651	JQ238733	JQ238819	JQ238906	JQ083502
Alocasia brancifolia (Schott) A. Hay	J. Bogner 1936 (M)	JQ238652	JQ238734	JQ238820	JQ238907	—
Alocasia brisbanensis (F. M. Bailey) Domin	J. Bogner 2363 (M)	JQ238653	JQ238735	JQ238821	—	JQ083503
Alocasia chaii P. Boyce	C. Lee AL-41 (SAR)	JQ238654	JQ238736	JQ238822	JQ238908	JQ083504
Alocasia clypeolata A. Hay	M. Medecilo 456 (De La Salle University Dasmariñas Herbarium)	JQ238655	JQ238737	JQ238823	JQ238909	JQ083505
Alocasia cucullata (Lour.) G. Don	J. Bogner 2638 (M)	JQ238656	JQ238738	JQ238824	JQ238910	JQ083506
Alocasia culionensis Engl.	M. Medecilo 360 (De La Salle University Dasmariñas Herbarium)	JQ238657	JQ238739	JQ238825	JQ238911	—
Alocasia cuprea K. Koch	P. Boyce et al. AL-1 (SAR)	JQ238658	JQ238740	JQ238826	JQ238912	JQ083507
Alocasia denudata Engl.	L. Nauheimer 98 (M)	JQ238659	JQ238741	JQ238827	JQ238913	JQ083514
Alocasia gageana Engl. & K. Krause	MO 78364	JQ238660	JQ238742	EU886580	AY248909	JQ238980
Alocasia grandis Clemenc.	BG Munich 02/2434	—	JQ238743	JQ238828	—	JQ083508
Alocasia heterophylla (C. Presl) Merr.	M. Medecilo 460 (De La Salle University Dasmariñas Herbarium)	JQ238661	JQ238744	JQ238829	JQ238914	JQ083509
Alocasia hollrungii A.Hay	DCN 2668 Edinburgh (E)	—	JQ238745	JQ238830	JQ238915	JQ083510
Alocasia hypnosa J.T.Yin, Y.H.Wang & Z.F.Xu	D. Prehsler 175 (WU)	JQ238662	JQ238746	JQ238831	JQ238916	JQ083582
Alocasia infernalis P. Boyce	C. Lee AL-16 (SAR)	JQ238663	JQ238747	JQ238832	JQ238917	JQ083511
Alocasia inornata Hallier f.	KEP 65175	JQ238664	JQ238748	JQ238833	—	JQ083512
Alocasia korthalsii Schott	L. Nauheimer 90 (M)	JQ238665	JQ238749	JQ238834	JQ238918	JQ083515
Alocasia lauterbachiana (Engl.) A. Hay	J. Bogner 1769 (M)	JQ238666	JQ238750	JQ238835	JQ238919	JQ083513
Alocasia longiloba Miq. (#1)	J. Bogner 2645 (M)	—	JQ238754	JQ238839	JQ238923	JQ083522
Alocasia longiloba Miq. (#2)	P. Boyce AL-193 (SAR)	JQ238667	JQ238751	JQ238836	JQ238920	JQ083519
Alocasia longiloba Miq. (#3)	P. Boyce & S. Y. Wong AL-257 (SAR)	JQ238669	JQ238753	JQ238838	JQ238922	JQ083521
Alocasia longiloba Miq. (#4)	DCN 2669 Edinburgh (E)	JQ238668	JQ238752	JQ238837	JQ238921	JQ083520
Alocasia lowii Hook.	P. Boyce AL-239 (SAR)	JQ238670	JQ238755	JQ238840	JQ238924	JQ083516
Alocasia macrorrhizos (L.) Don	M. Medecilo 435 (De La Salle University Dasmariñas Herbarium)	JQ238671	JQ238756	JQ238841	JQ238925	JQ083523
Alocasia maquilingensis Merr.	M. Medecilo 468 (De La Salle University	JQ238672	JQ238757	JQ238842	JQ238926	JQ083524

	Dasmariñas Herbarium)					
Alocasia melo A. Hay, P. Boyce & K. Wong	C. Lee AL-61 (SAR)	JQ238673	JQ238758	JQ238843	JQ238927	JQ083525
Alocasia micholitziana Sander	M. Medecilo 465 (De La Salle University Dasmariñas Herbarium)	JQ238674	JQ238759	JQ238844	—	JQ083526
Alocasia monticola A. Hay	D. Scherberich 761 (LYJB)	JQ238675	JQ238760	JQ238845	JQ238928	JQ083527
Alocasia navicularis (K. Koch & C.D. Bouché) K. Koch & C.D. Bouché	T. Croat 78014 (MO)	JQ238676	JQ238761	EU886581	AY248925	JQ238981
Alocasia nebula A. Hay	C. Lee AL-23 (SAR)	JQ238677	JQ238762	JQ238846	JQ238929	JQ083528
Alocasia nycteris Medecilo, G. C. Yao & Madulid	M. Medecilo 458 (De La Salle University Dasmariñas Herbarium)	JQ238678	JQ238763	JQ238847	JQ238930	JQ083529
Alocasia odora (Lindl.) K. Koch	P. Boyce s.n. (QSBG)	JQ238679	JQ238764	JQ238848	JQ238931	JQ083530
Alocasia pangeran A. Hay	P. Boyce et al. AL-6 (SAR)	JQ238680	JQ238765	JQ238849	JQ238932	JQ083531
Alocasia peltata M. Hotta	L. Nauheimer 66 (M)	JQ238681	JQ238766	JQ238850	JQ238933	JQ083532
Alocasia perakensis Hemsl.	K. Larsen 42938 (AAU)	—	JQ238767	JQ238851	—	JQ083533
Alocasia plumbea Van Houtte	J. Bogner 2960 (M)	JQ238682	JQ238768	JQ238852	JQ238934	JQ083534
Alocasia portei Schott	M. Medecilo 301 (De La Salle University Dasmariñas Herbarium)	JQ238683	JQ238769	JQ238853	JQ238935	JQ083535
Alocasia princeps W. Bull	P. Boyce AL-195 (SAR)	JQ238684	JQ238770	JQ238854	JQ238936	JQ083536
Alocasia principiculus A. Hay	L. Nauheimer 100 (M)	JQ238685	JQ238771	JQ238855	JQ238937	JQ083537
Alocasia ramosii A. Hay	M. Medecilo 469 (De La Salle University Dasmariñas Herbarium)	JQ238686	JQ238772	JQ238856	JQ238938	JQ083538
Alocasia reginae N. E. Br.	P. Boyce AL-197 (SAR)	JQ238687	JQ238773	JQ238857	JQ238939	JQ083539
Alocasia reginula A. Hay	J. Yeo Al-24 (SAR)	JQ238688	JQ238774	JQ238858	JQ238940	JQ083540
Alocasia reversa N. E. Br.	R. Kiew, J. Tan, J. Sang AL-93 (SAR)	JQ238689	JQ238775	JQ238859	JQ238941	JQ083541
Alocasia ridleyi A. Hay	J. Bogner 2735 (M)	JQ238690	JQ238776	JQ238860	JQ238942	JQ083542
Alocasia robusta M. Hotta (‚red Sabah‘)	L. Nauheimer 103 (M)	—	—	JQ238862	JQ238944	JQ083543
Alocasia robusta M. Hotta (‚white Sabah‘)	L. Nauheimer 106 (M)	—	—	JQ238863	JQ238945	JQ083544
Alocasia robusta M. Hotta (‚red Sarawak‘)	P. Boyce AL-43 (SAR)	JQ238691	JQ238777	JQ238861	JQ238943	JQ083545
Alocasia sanderiana W. Bull	M. Medecilo 384 (De La Salle University Dasmariñas Herbarium)	JQ238692	JQ238778	JQ238864	JQ238946	JQ083546
Alocasia sarawakensis M. Hotta	P. Boyce AL-199 (SAR)	JQ238693	JQ238779	JQ238865	JQ238947	—
Alocasia scabriuscula N. E. Br.	L. Nauheimer 33 (M)	JQ238694	JQ238780	JQ238866	JQ238948	JQ083547
Alocasia scalprum A. Hay	M. Medecilo 432 (De La Salle University Dasmariñas Herbarium)	JQ238695	JQ238781	JQ238867	JQ238949	JQ083548
Alocasia sinuata N. E. Br.	M. Medecilo 391 (De La Salle University Dasmariñas Herbarium)	JQ238696	JQ238782	JQ238868	JQ238950	JQ083549
Alocasia sp.nov. Bo011	BG Bogor XI-B-VII 267 photo available	JQ238697	JQ238783	JQ238869	JQ238951	JQ083551
Alocasia sp.nov. Bo07	BG Bogor XI-B-IX 250 photo available	JQ238698	JQ238784	JQ238870	JQ238952	JQ083552
Alocasia sp.nov. Gomantong	L. Nauheimer 102 (M)	JQ238699	JQ238785	JQ238871	JQ238953	JQ083553
Alocasia sp.nov. inopinata P. Boyce	P. Boyce AL-191 (SAR)	JQ238707	JQ238793	JQ238879	JQ238961	JQ083554
Alocasia sp.nov. kelamensis P. Boyce	BG Bogor photo available	JQ238708	JQ238794	JQ238880	JQ238962	JQ083555
Alocasia sp.nov. Kerby	Kerby 183 (M)	JQ238700	JQ238786	JQ238872	JQ238954	JQ083556
Alocasia sp.nov. kulat P. Boyce	P. Boyce AL-207 (SAR)	JQ238709	JQ238795	JQ238881	JQ238963	JQ083557

Alocasia sp.nov. MPM1	M. Medecilo 405 (De La Salle University Dasmariñas Herbarium)	JQ238701	JQ238787	JQ238873	JQ238955	JQ083558
Alocasia sp.nov. MPM2	M. Medecilo 399 (De La Salle University Dasmariñas Herbarium)	JQ238702	JQ238788	JQ238874	JQ238956	—
Alocasia sp.nov. MPM3	M. Medecilo 473 (De La Salle University Dasmariñas Herbarium)	JQ238703	JQ238789	JQ238875	JQ238957	JQ083559
Alocasia sp.nov. MPM4	M. Medecilo 474 (De La Salle University Dasmariñas Herbarium)	JQ238704	JQ238790	JQ238876	JQ238958	JQ083560
Alocasia sp.nov. ridleythai	P. Boyce s.n. (QSBG)	JQ238710	JQ238796	JQ238882	JQ238964	JQ083550
Alocasia sp.nov. Septier	D. Scherberich 760 (LYJB)	JQ238705	JQ238791	JQ238877	JQ238959	JQ083561
Alocasia sp.nov. Setiam	L. Nauheimer 82 (M)	JQ238706	JQ238792	JQ238878	JQ238960	JQ083562
Alocasia suhirmaniana Yuzammi & A. Hay	BG Bogor photo available	JQ238711	JQ238797	JQ238883	JQ238965	JQ083563
Alocasia warburgii Engl.	Seidenschwarz s.n. (M)	JQ238712	JQ238798	JQ238884	JQ238966	JQ083564
Alocasia watsoniana Sander (#1)	P. Boyce et al. AL-119 (SAR)	JQ238714	JQ238800	JQ238886	JQ238968	JQ083517
Alocasia watsoniana Sander (#2)	L. Nauheimer 84 (M)	JQ238713	JQ238799	JQ238885	JQ238967	JQ083518
Alocasia wongii A. Hay	L. Nauheimer 113 (M)	JQ238715	JQ238801	JQ238887	JQ238969	JQ083565
Alocasia zebrina Schott ex Van Houtte	M. Medecilo 459 (De La Salle University Dasmariñas Herbarium)	JQ238716	JQ238802	JQ238888	JQ238970	JQ083566
Ariopsis protanthera N. E. Br.	H. Hara 1960 (TI)	AY248985	AY248947	EU886587	AY248910	JQ083567
Arisaema speciosum (Wall.) Mart. ex Schott & Endl.	W. Hetterscheid s.n.	AY275609	AY275609	EU886502	AY279168	EU886470
Arum italicum Mill.	BG Mainz 20Jul2001	AY248997	AY248959	EU886517	AY248922	EU886472
Biarum davisii Turrill	T. Croat 78231 (MO)	AY248998	AY248960	EU886525	AY248923	EU886479
Colocasia affinis var. *jenningsii* Schott	J. Bogner 2652 (M)	JQ238717	JQ238803	JQ238889	JQ238971	JQ083568
Colocasia esculenta (L.) Schott	J. Bogner 2958 (M)	JQ238718	JQ238804	JQ238890	JQ238972	JQ083569
Colocasia fallax Schott	J. Bogner 1139 (M)	JQ238719	JQ238805	JQ238891	JQ238973	—
Colocasia fontanesii Schott	J. Bogner 2215 (M)	JQ238720	JQ238806	JQ238892	JQ238974	JQ083570
Colocasia gigantea (Blume) Hook.f.	J. Bogner 427 (M)	JQ238721	JQ238807	JQ238893	JQ238975	JQ083571
Colocasia menglaensis J. T. Yin , H. Li & Z. F. Xu	J. Bogner 2274 (M)	JQ238722	JQ238808	JQ238894	JQ238976	JQ083572
Colocasia sp. nov. Boyce Th2	P. Boyce s.n. (QSBG)	JQ238723	JQ238809	JQ238895	JQ238977	JQ083573
Dacunculus vulgaris Schott	T. Croat 78286 (MO)	AY249002	AY248964	EU886532	AY248927	EU886476
Eminium spiculatum (Blume) Schott	BG Bonn 15031	AY249003	AY248965	EU886530	AY248928	EU886474
Helicodiceros muscivorus (L. f.) Engl.	T. Croat 71821 (MO)	AY249004	AY248966	EU886533	AY248929	EU886480
Lazarum brownii Schott	W. Hetterscheid HAR43	AY249013	AY248975	EU886538	EU886607	EU886492
Pinellia ternata (Thunb.) Ten. ex Breitenb.	J. McClemens s.n. 30Jul2001	AY249006	AY248968	EU886503	AY248931	JQ083574
Protarum sechellarum Engl.	J. Bogner s.n. (M)	JQ238724	JQ238810	—	—	JQ083576
Remusatia pumila (D. Don) H. Li & A. Hay	K. Vainio-Mattila 90-201 (M)	JQ238725	JQ238811	JQ238896	JQ238978	JQ083577
Remusatia vivipara (Roxb.) Schott	J. Bogner 2982 (M)	JQ238726	JQ238812	JQ238897	JQ238979	JQ083578
Sauromatum giganteum (Engl.) Cusimano & Hett.	J. W. Waddick s.n. 20Aug2001	AY249013	AY248975	EU886536	AY248938	EU886490
Steudnera assamica Hook. f.	J. Bogner 2588 (M)	EF517219	EF517214	JQ238898	EF517224	JQ083579
Steudnera discolor W. Bull	J. Bogner 1582 (M)	EF517216	EF517211	EU886586	EF517221	JQ083580
Steudnera kerrii Gagnep.	J. Bogner 1891 (M)	EF517218	EF517213	JQ238899	EF517223	JQ083581
Theriophonum dalzellii Schott	P. Bruggemann 168	AY249011	AY248973	EU886534	AY248936	EU886486
Typhonium trilobatum (L.) Schott	J. Murata 5	AY249016	AY248978	EU886571	AY248941	EU886496

Table S2. Crown ages of the main clades in all 15 topologies of the four basal clades (*Alocasia* / *Colocasia gigantea* (a), Areae clade (b), *Colocasia* clade (c), and *Alocasia hypnosa* (d)) under strict clock model (i) and relaxed model (ii). Dates are in million years before present with 95% highest posterior density intervals in parentheses. The lowest value of the estimated samples size (ESS) values is given.

i) Strict clock model

Topology	Lowest ESS	Clock rate	*Alocasia*	*Alocasia* / *C. gigantea* (a)	Areae clade (b)	*Colocasia* clade (c)	*A. hypnosa* (d)	Ingroup
(ab)(cd)	174	6.13E-4	12.88 (9.11 – 16.98)	22.40 (15.14 – 30.23)	37.13 (30.79 – 43.36)	23.05 (15.32 – 30.77)	40.41 (34.20 – 46.69)	41.13 (34.90 – 47.20)
(ac)(bd)	186	6.12E-4	12.60 (8.76 – 16.38)	20.99 (14.28 – 28.31)	37.76 (31.69 – 43.86)	26.16 (18.34 – 35.04)	28.52 (18.65 – 38.92)	41.85 (35.87 – 47.29)
(ad)(bc)	188	6.12E-4	13.08 (9.20 – 17.29)	23.83 (15.82 – 32.55)	36.76 (30.04 – 43.00)	22.80 (15.61 – 30.46)	31.88 (23.22 – 41.39)	40.71 (34.23 – 47.05)
a(b(cd))	127	5.97E-4	13.40 (9.44 – 17.46)	24.25 (16.23 – 32.94)	36.33 (30.27 – 42.60)	26.09 (18.01 – 34.44)	39.38 (33.47 – 45.79)	40.76 (35.02 – 47.13)
a(c(bd))	148	6.05E-4	13.29 (9.38 – 17.78)	24.03 (15.69 – 32.72)	35.93 (28.97 – 42.90)	25.51 (17.93 – 34.35)	39.48 (32.75 – 46.73)	40.24 (33.56 – 47.21)
a(d(bc))	82	5.89E-4	13.14 (9.53 – 17.01)	21.98 (15.56 – 28.96)	43.63 (40.36 – 46.70)	20.36 (14.43 – 26.94)	26.86 (19.99 – 34.52)	47.30 (46.90 – 47.56)
b(a(cd))	555	5.90E-4	12.85 (9.40 – 16.48)	20.48 (14.69 – 26.95)	43.53 (40.24 – 46.59)	22.35 (15.67 – 29.45)	26.48 (18.67 – 33.64)	47.28 (46.94 – 47.55)
b(c(ad))	705	5.88E-4	13.03 (9.38 – 16.82)	21.22 (14.81 – 27.64)	43.56 (40.25 – 46.71)	20.94 (14.42 – 27.46)	30.36 (22.40 – 38.87)	47.30 (46.94 – 47.56)
b(d(ac))	524	5.96E-4	13.40 (9.50 – 17.74)	24.13 (16.32 – 32.97)	36.01 (29.86 – 42.02)	27.14 (18.97 – 36.17)	38.98 (32.62 – 45.24)	41.06 (34.94 – 47.22)
c(a(bd))	200	6.14E-4	12.51 (8.82 – 16.25)	20.76 (13.90 – 27.87)	37.12 (31.15 – 42.88)	26.92 (18.48 – 35.87)	28.26 (18.57 – 38.23)	41.78 (35.96 – 47.22)
c(b(ad))	333	6.00E-4	13.49 (9.61 – 17.99)	24.11 (16.26 – 32.58)	35.99 (29.37 – 41.89)	27.20 (18.34 – 35.85)	39.62 (33.22 – 45.87)	41.07 (34.89 – 47.21)
c(d(ab))	172	5.99E-4	13.38 (9.43 – 17.82)	24.16 (16.55 – 33.76)	36.30 (29.98 – 42.55)	25.81 (17.94 – 34.26)	40.78 (34.91 – 47.24)	40.78 (34.91 – 47.24)
d(a(bc))	179	6.09E-4	13.02 (9.16 – 16.99)	22.52 (15.29 – 30.17)	37.37 (31.21 – 43.39)	23.18 (15.56 – 30.63)	41.46 (35.60 – 47.30)	41.46 (35.60 – 47.30)
d(b(ac))	260	5.96E-4	13.44 (9.46 – 17.72)	24.18 (15.93 – 32.61)	36.44 (30.23 – 42.60)	26.19 (18.43 – 34.96)	40.98 (34.96 – 47.22)	40.98 (34.96 – 47.22)
d(c(ab))	202	5.89E-4	13.00 (9.62 – 16.79)	21.25 (14.90 – 27.93)	43.57 (40.20 – 46.55)	21.34 (14.61 – 28.45)	26.47 (18.68 – 34.17)	47.28 (46.94 – 47.56)
mean		**6.02E-4**	**13.11 (9.30 – 17.20)**	**22.85 (15.48 – 30.83)**	**38.05 (32.34 – 43.63)**	**24.45 (16.85 – 32.49)**	**35.04 (27.75 – 42.63)**	**42.31 (37.36 – 47.28)**
stdev		**9.28E-6**	**0.30 (0.25 – 0.56)**	**1.44 (0.79 – 2.34)**	**2.91 (4.17 – 1.65)**	**2.31 (1.67 – 3.14)**	**5.87 (7.07 – 4.79)**	**2.61 (4.98 – 0.16)**

ii) Relaxed clock model

Topology	Lowest ESS	Mean Rate	*Alocasia*	*Alocasia* / *C. gigantea* (a)	Areae clade (b)	*Colocasia* clade (c)	*A. hypnosa* (d)	Ingroup
(ab)(cd)	248	5.69E-4	19.01 (11.18 – 27.80)	29.22 (17.97 – 40.73)	32.97 (23.07 – 41.91)	23.60 (13.39 – 34.91)	34.00 (22.20 – 45.38)	40.17 (30.10 – 47.32)
(ac)(bd)	284	5.60E-4	19.07 (11.64 – 27.30)	28.63 (17.66 – 39.63)	33.48 (24.83 – 42.19)	24.86 (14.04 – 36.09)	39.12 (29.97 – 46.56)	40.73 (31.87 – 47.39)
(ad)(bc)	387	5.56E-4	19.00 (11.47 – 26.92)	28.19 (17.07 – 38.77)	33.83 (25.10 – 42.57)	26.19 (14.96 – 37.68)	35.92 (24.97 – 46.34)	41.04 (32.14 – 47.38)
a(b(cd))	333	5.66E-4	19.38 (11.42 – 27.89)	30.22 (19.21 – 42.53)	32.81 (23.20 – 42.67)	23.30 (12.58 – 33.58)	32.93 (21.43 – 44.56)	40.15 (29.89 – 47.45)
a(c(bd))	303	5.74E-4	19.14 (10.63 – 27.81)	29.73 (17.98 – 41.57)	31.22 (21.35 – 40.53)	25.01 (13.45 – 36.54)	36.38 (26.42 – 45.60)	39.60 (29.52 – 47.33)
a(d(bc))	317	5.58E-4	19.73 (11.77 – 28.59)	30.61 (19.04 – 41.93)	32.14 (22.46 – 40.97)	25.21 (14.35 – 36.71)	38.85 (29.25 – 46.96)	40.57 (30.98 – 47.48)
b(a(cd))	608	4.97E-4	20.98 (13.41 – 29.02)	31.66 (21.21 – 42.43)	40.25 (34.30 – 45.99)	25.17 (15.22 – 35.76)	35.34 (24.36 – 45.84)	47.26 (46.95 – 47.53)
b(c(ad))	653	4.96E-4	20.48 (13.45 – 28.59)	29.79 (20.03 – 40.12)	40.28 (34.00 – 45.58)	27.83 (17.00 – 39.33)	36.88 (26.59 – 46.29)	47.25 (46.95 – 47.55)
b(d(ac))	633	5.01E-4	20.39 (13.26 – 28.41)	30.17 (20.23 – 40.31)	40.14 (33.75 – 45.62)	26.20 (15.94 – 36.71)	40.97 (31.04 – 47.43)	47.25 (46.95 – 47.54)
c(a(bd))	231	5.67E-4	19.18 (11.30 – 27.93)	28.98 (17.60 – 40.01)	31.26 (22.03 – 40.51)	27.05 (14.89 – 39.46)	36.25 (26.17 – 45.26)	40.51 (30.63 – 47.41)
c(b(ad))	379	5.74E-4	18.15 (11.06 – 25.84)	26.59 (16.92 – 37.32)	32.28 (23.26 – 41.40)	26.82 (15.14 – 39.49)	33.40 (22.56 – 43.90)	40.50 (31.14 – 47.43)
c(d(ab))	264	5.69E-4	18.85 (11.39 – 26.94)	28.30 (18.36 – 38.87)	31.24 (22.21 – 39.95)	26.93 (14.84 – 39.25)	37.76 (28.68 – 46.24)	40.59 (31.50 – 47.31)
d(a(bc))	205	5.79E-4	18.81 (10.94 – 27.76)	28.76 (17.41 – 40.53)	31.24 (21.23 – 41.09)	24.37 (13.48 – 35.62)	39.52 (29.07 – 47.45)	39.52 (29.07 – 47.45)
d(b(ac))	260	5.76E-4	18.33 (11.00 – 26.13)	27.49 (17.23 – 38.20)	32.88 (23.66 – 41.91)	23.82 (13.89 – 35.30)	40.21 (30.68 – 47.40)	40.21 (30.68 – 47.40)
d(c(ab))	295	5.75E-4	18.62 (10.67 – 26.36)	28.33 (17.63 – 39.41)	31.65 (22.39 – 41.33)	25.39 (14.01 – 37.15)	40.07 (30.21 – 47.27)	40.07 (30.21 – 47.27)
mean		**5.54E-04**	**19.28 (11.64 – 27.55)**	**29.11 (18.37 – 40.16)**	**33.84 (25.12 – 42.28)**	**25.45 (14.48 – 36.91)**	**37.17 (26.91 – 46.16)**	**41.70 (33.91 – 47.41)**
stdev		**3.00E-05**	**0.80 (0.95 – 0.95)**	**1.29 (1.29 – 1.53)**	**3.40 (4.73 – 1.94)**	**1.36 (1.12 – 1.82)**	**2.58 (3.24 – 1.08)**	**2.90 (6.80 – 0.09)**

Table S3. Clade support, divergence time estimates and ancestral area reconstruction for *Alocasia* and its outgroup obtained with S-DIVA and Lagrange. Node numbers refer to Figure 4. The column ‚Split' represents the estimated ancestral areas for the branches following the respective node. Vertical bars separate upper branches (left) from lower branches (right). Only estimates within one log-likelihood unit of the optimal value are given. Differences in the optimal reconstruction of Lagrange and S-DIVA are indicated in bold.

	BEAST		**Lagrange**			**S-DIVA**		
Node # (Fig.4)	Posterior probability	Age in Ma (95% HPD interval)	Split	Relative probablity [%]	lnL	Area	Relative probablity [%]	*P*
1 fossil calibration	1	47.25 (47 – 47.6)	[H|A] [A|A] [AH|A]	32 26 19	-153.1 -153.3 -153.6	AH	100	1
2	1	41.07 (34.9 – 47.2)	[A|A]	81	-152.1	A	100	1
3	1	27.2 (18.3 – 35.9)	[A|A]	75	-152.2	A	100	1
4	1	12.46 (7.4 – 17.7)	[A|A]	92	-152	A	100	1
5	1	6.51 (3.2 – 10.2)	[A|A]	98	-151.9	A	100	1
6	0.4	4.88 (2.1 – 8)	[A|A]	99	-151.9	A	100	0.43
7	0.9	2.33 (0.4 – 4.5)	[A|A]	100	-151.9	A	100	0.9
8	0.2	1.5 (0.1 – 3.2)	[A|A]	100	-151.9	A	100	0.19
9	1	7.03 (3.4 – 10.7)	[A|A]	98	-151.9	A	100	1
10	1	3.79 (1 – 6.9)	[A|A]	99	-151.9	A	100	0.98
11	1	1.97 (0.4 – 3.9)	[A|A]	100	-151.9	A	100	1
12	0.7	0.73 (0 – 2)	[A|A]	100	-151.9	A	100	0.7
13	1	39.62 (33.2 – 45.9)	[A|A]	92	-152	A	100	1
14	1	38.97 (32.8 – 45.5)	[A|A]	97	-152	A	100	1
15	1	35.99 (29.4 – 41.9)	[A|A]	96	-152	A	100	1
16	0.8	33.08 (26.7 – 39.7)	[A|A]	92	-152	A	100	0.79

17	1	28.52 (22.7 – 34.3)	[A|A]	85	-152.1	A	100	1
18	0.9	24.73 (19.2 – 31.2)	[A|A]	78	-152.2	A AG	92.69 7.31	0.92
19	0.9	21.42 (15.9 – 26.7)	[A|A] [A|G]	40 32	-152.8 -153.1	AG	100	0.9
20	1	16.73 (12.3 – 21.3)	[G|G] [G|AG]	48 42	-152.7 -152.8	G AG	81.32 18.68	1
21	0.2	15.82 (11.6 – 20.4)	[G|G] [AG|G]	54 26	-152.5 -153.3	G	100	0.19
22	0.2	14.92 (10.5 – 19.3)	[G|G]	85	-152.1	G	100	0.23
23	0.9	12.97 (8.7 – 17.5)	[G|G]	94	-152	G	100	0.9
24	**1**	**9.82 (3.8 – 16.3)**	**[B|A]**	**65**	**-152.3**	**AF**	**100**	**1**
25 *Alocasia* stem	1	24.11 (16.3 – 32.6)	[A|A] [A|B] [A|AB]	40 22 16	-152.8 -153.4 -153.7	A AB	71.88 28.12	1
26 ***Alocasia*** **crown**	**1**	**13.49 (9.6 – 18)**	**[B|B]** **[AB|B]** **[B|AB]**	**33** **31** **17**	**-153** **-153.1** **-153.7**	**A** **AB** **B**	**51.33** **26.73** **21.94**	**1**
27 clade A	0.9	9.86 (6.3 – 13.6)	[B|B] [B|AB]	54 37	-152.5 -152.9	AB B	57.47 42.53	0.94
28	0.2	8.76 (5.7 – 12.5)	[B|B]	44	-152.7	B A AB	42.34 31.21 26.45	0.22
29	0.2	7.2 (4.2 – 11)	[B|A]	57	-152.5	AB	100	0.15
30	1	3.48 (1.1 – 6.2)	[A|A]	92	-152	A	100	1
31	0.4	2.21 (0.5 – 4.2)	[A|A]	99	-151.9	A	100	0.45
32	0.2	1.31 (0 – 2.9)	[A|A]	100	-151.9	A	100	0.22
33	0.3	6.61 (3.8 – 9.8)	[B|B] [A|AB] [B|AB]	37 16 16	-152.9 -153.7 -153.7	B AB A	42.49 32.03 25.48	0.29
34	0.4	3.92 (1.2 – 6.8)	[A|B]	72	-152.2	AB	100	0.41
35	0.3	5.17 (2.8 – 8)	[A|B]	81	-152.1	AB	100	0.32
36	0.2	3.92 (1.7 – 6.4)	[C|B] [B|B]	56 37	-152.5 -152.9	BC	100	0.23

37		1	2.22 (0.6 – 4.1)		[B|B]	99	-151.9	B	100	1
38		0.5	1.22 (0.1 – 2.7)		[B|B]	100	-151.9	B	100	0.51
39		1	3.04 (1.1 – 5.2)		[A|A]	93	-152	A	100	0.96
40		0.5	1.97 (0.3 – 3.8)		[A|A]	99	-151.9	A	100	0.52
41		**0.9**	**11.28 (8 – 14.8)**		**[B|B]** **[B|AB]** **[BC|B]**	**41** **24** **19**	**-152.8** **-153.3** **-153.6**	**A** **C** **B** **AB**	**46.59** **31.08** **20.21** **2.13**	**0.92**
42		0.3	10.36 (7.5 – 13.9)		[C|BC]	68	-152.3	C AB	99.59 0.41	0.31
43 clade B		0.9	8.47 (5.5 – 11.6)		[B|C]	78	-152.2	BC AB AC	34.63 33.25 32.12	0.94
44		0.9	5.71 (3 – 8.6)		[C|C]	85	-152.1	C	100	0.91
45		1	3.69 (1.4 – 6.2)		[C|C] [C|CD]	78 20	-152.2 -153.5	C	100	0.99
46		1	1.34 (0 – 3)		[C|C]	93	-152	C	100	1
47		0.3	7.22 (4.2 – 10.3)		[A|B] [A|A]	64 28	-152.4 -153.2	AB	100	0.35
48		1	2.92 (0.9 – 5.1)		[B|B]	99	-151.9	B	100	1
49		1	1.46 (0.1 – 3)		[B|B]	100	-151.9	B	100	0.99
50 clade C		1	7.24 (4.4 – 10.3)		[D|C] [C|C]	41 19	-152.8 -153.6	CD DE DF EF	36.01 24.33 22.38 17.29	1
51		1	2.62 (0.6 – 4.9)		[D|D]	87	-152.1	D	100	1
52		0.2	6.1 (3.6 – 9)		[C|E]	73	-152.2	CE CF EF	39.65 37.57 22.79	0.23
53		0.3	4.8 (2.3 – 7.9)		[F|E] [E|E]	47 42	-152.7 -152.8	EF	100	0.34
54		1	1.44 (0.1 – 3.3)		[E|E]	99	-151.9	E	100	1
55		0.9	8.78 (6 – 12.2)		[A|B] [B|B]	44 39	-152.8 -152.9	AB A	78.55 21.45	0.87

56 clade D	1	6.33 (4.1 – 8.7)	[B|B]	63	-152.4	B C AB	58.04 30.42 11.53	1
57	0	5.06 (3.5 – 7.1)	[BC|C] [B|B]	49 19	-152.6 -153.6	C B AB	59.45 34.03 6.51	0.05
58	0	3.79 (2.2 – 6)	[C|B]	92	-152	BC AB AC	51.07 30.71 18.23	0.01
59	0	2.85 (1.4 – 5.1)	[B|B]	57	-152.5	B AB A	49.23 37.84 12.93	0.03
60	0.3	0.86 (0 – 2.4)	[B|A]	95	-152	AB	100	0.35
61	0.1	2.68 (0.7 – 5)	[A|B] [B|B]	52 42	-152.6 -152.8	AB	100	0.06
62	1	1.26 (0 – 2.9)	[B|B]	99	-151.9	B	100	0.99
63	0.1	2.95 (0.9 – 5.2)	[C|C]	96	-152	C	100	0.06
64	0	4.25 (2.3 – 6.5)	[C|C] [BC|C]	55 43	-152.5 -152.8	C	100	0.01
65	0.9	2.86 (1.2 – 4.8)	[C|C]	100	-151.9	C	100	0.94
66	1	0.51 (0 – 1.4)	[C|C]	100	-151.9	C	100	1
67	0.2	2.2 (0.7 – 3.8)	[C|C]	100	-151.9	C	100	0.22
68	1	0.92 (0 – 2.1)	[C|C]	100	-151.9	C	100	1
69	0.4	1.25 (0.1 – 2.7)	[C|C]	100	-151.9	C	100	0.35
70	0.1	3.03 (1.1 – 5.3)	[C|B]	83	-152.1	BC	100	0.06
71	1	1.24 (0 – 2.9)	[B|B]	96	-152	B	100	0.98
72	0.1	4.87 (2.9 – 6.8)	[B|B]	74	-152.2	B	100	0.06
73	0.9	3.33 (1.5 – 5.2)	[C|B]	74	-152.2	BC	100	0.91
74	0.3	2.59 (0.9 – 4.3)	[B|B]	99	-151.9	B	100	0.3
75	0.3	1.29 (0.1 – 2.7)	[B|B]	100	-151.9	B	100	0.27
76	0.2	1.75 (0.2 – 3.4)	[B|B]	100	-151.9	B	100	0.18
77	0.9	3.39 (1.4 – 5.4)	[B|B]	87	-152.1	B	100	0.92
78	1	1.99 (0.5 – 3.6)	[B|B]	100	-151.9	B	100	0.99
79	0.5	1.12 (0.1 – 2.4)	[B|B]	100	-151.9	BD	100	0.98
80	1	1.27 (0 – 2.8)	[D|B]	93	-152	B	100	0.5

4

Discussion

Molecular Phylogenetics and Systematics

The molecular phylogeny presented in Chapter 2 (Figure 2) represents the most comprehensive phylogeny of the Araceae family to date, with 132 accessions representing 117 of 118 genera. It enlarges the phylogeny of Cusimano et al. (2011) by including *Apoballis*, *Hestia*, *Ooia*, and *Pichinia*, and therefore contains all genera of the family except for the recently described monotypic *Lorenzia* (Gonçalves, 2012).

The molecular phylogenies presented in Chapter 3 (Figure 3) are the first attempt to investigate species relationships within the genus *Alocasia* and include 71 of the 113 species represented by 78 accessions. They also include 11 of 28 species of the *Colocasia* clade, which was thought to be closely related to *Alocasia* based on morphology (Engler and Krause, 1920; Mayo et al., 1997).

Polyphyletic genera My phylogenetic analyses (Chapters 2 and 3) revealed the non-monophyly of four genera, *Homalomena* and *Nephthytis*, both with geographically disjunct distributions, and the two morphologically similar genera *Alocasia* and *Colocasia*. The non-monophyly of the American and Asian species of *Homalomena* had been discovered already by Gauthier et al. (2008) in their attempt to reorganize the highly diverse genus *Philodendron*. However, their sampling was insufficient (most importantly it lacked the Asian genus *Furtadoa*) and statistical support was not high enough to separate the non-monophyletic *Homalomena* into an Asian *Homalomena* and an American *Adelonema* (this name would be the oldest available generic name for the group). Surprisingly, the only Southeast Asian species of *Nephthytis* (*N. bintuluensis*) groups with *Aglaodorum* and *Aglaonema* (both occurring in the same region), while the African *Nephthytis afzelii* groups with the African genera *Anchomanes* and *Pseudohydrosme*. The *Amorphophallus* clade shows a geographical signal in the phylogenies of Sedayu et al. (2010), with the African species of *Amorphophallus* sister to the remaining species in this genus. Sedayu et al. also found *Pseudodracontium* embedded in *Amorphophallus*, a result not visible in the more coarsely sampled phylogeny presented here (Chapter 2, Figure 2). *Spathiphyllum* is the only geographically disjunct genus that my study does not sample across its range. Therefore, the relationship between the two Southeast Asian species, the tropical American species currently placed in *Spathiphyllum* (47 species), and its monotypic sister genus *Holochlamys* from New Guinea remains to be tested.

The polyphyly of *Alocasia* and *Colocasia* does not concern disjunctly distributed species, but stems from the morphological circumscription of these genera. My dense sampling of *Alocasia* and its outgroups (Chapter 3) revealed this polyphyly. To maintain the monophyly of *Alocasia*, *A. hypnosa* probably has to be removed from the genus, although my data do not resolve the final placement of *A. hypnosa*. It was described in 2005 from plants collected in southern Yunnan, China, and later cultivated at the Xishuangbanna Botanical Garden (Wang et al., 2005). *Alocasia hypnosa* is characterized by a purple spathe, numerous long stolons, and deciduousness and was placed in *Alocasia* because of its few basal ovules, red colored fruits, and its overall similarity to *Alocasia odora*. My data show that this species is highly divergent and does not group with any of the major clades in the *Pistia* clade (nuclear and chloroplast data; in Chapter 3, Figure 3, red colored branch). A clearly misplaced species is *Colocasia gigantea*, which does not group with the type species of *Colocasia*, but is sister to *Alocasia*. It occurs naturally from south-west China, Indochina, and Thailand through Peninsular Malaysia and Sumatra to Java. This large-growing species was originally described as *Caladium giganteum* (Blume, 1823); Schott (1857) then made it the basis of a new genus, *Leucocasia*, recognizing that it did not fit in *Caladium* due to its unilocular ovaries with sub-orthotropous ovules. Later, Hooker (1893) transferred the species to *Colocasia* where it indeed fit well in terms of its placentation and leaf thickness. The placentation and the dispersal syndrome is often used to distinguish *Alocasia* from

Colocasia (Hay, 1998); basal placentation of few reddish-colored fruits with few big seeds, which are mainly dispersed by birds in *Alocasia*, contrast with the parietal placentation in many whitish-colored fruits with many small seeds, mainly dispersed by mammals in *Colocasia*. These characters, however, are plastic. Even after removal of *C. gigantea*, the circumscriptions of the genera *Colocasia*, *Remusatia*, and *Steudnera* remain problematic. Nuclear and plastid phylogenies (Chapter 3, Figure 3) show two clades of *Colocasia* species, and also of *Remusatia*. A recent attempt to clarify the phylogenetic status of *Remusatia* by Li et al. (2011) failed due to lack of phylogenetic resolution and insufficient sampling of the outgroup.

Hybridization and chloroplast capture The comparison of nuclear and chloroplast phylogenies of *Alocasia* revealed major topological incongruencies (Chapter 3, Figure 3). Most taxa in the plastid phylogeny group according to their geographic origin, while many clades in the nuclear phylogeny share morphological characters. This is especially obvious in the two *Alocasia* groups that are represented by multiple accessions in the phylogeny, *A. robusta* and the so-called *longiloba* group (Hay, 1998). Similar geographic signal in plastid sequence data, but morphology matching nuclear signal has been found in *Heuchera* group (Soltis and Kuzoff, 1995), *Nothofagus* (Cristina Acosta and Premoli, 2010), *Ilex* (Manen et al., 2010), *Silene* (Rautenberg et al., 2010), and for the Southeast Asian *Lithocarpus* (Cannon and Manos, 2003) and *Macaranga* (Baenfer et al., 2006). Hybridization can cause this pattern under certain conditions, for example when male function in hybrids is reduced (because of infertile pollen) and there is continuous backcrossing with the paternal parent (Tsitrone et al., 2003). A species arriving in a new area may then take over the maternally inherited plastid but maintain its nuclear genome. This scenario seems plausible in *Alocasia*, where hybridization in cultivated species is common even between distantly related species, such as *A. macrorrhizos* and *A. odora* (Garner, 2010; pers. comm., February 2011). Moreover, the pollinator species of the genus *Colocasiomyia* are known to visit several *Alocasia* species within an area (Toda and Lakim, 2011). The nuclear phylogeny is therefore more reliable for interpreting the evolution of *Alocasia*. The study in Chapter 3 demonstrates the importance of using biparentally inherited nuclear DNA and the danger of relying exclusively on plastid DNA for evolutionary studies, which is a common practice in molecular systematics, especially when a study is relying on herbarium material where nuclear sequences are usually difficult to obtain.

Divergence Dating

The divergence dating for the two groups, the Araceae family and the *Alocasia* alliance, presented in Chapters 2 and 3 relied on multiple analyses using several molecular clock models, prior distributions, and calibration schemes. Comparison of different approaches and methods contributed to the proper assessment of the results and reliable age estimates.

Fossil calibration The basis for the dating of the Araceae family phylogeny was a critical assessment of the fossil record (Chapter 2, Supplementary Table 1). Seven fossils were used as minimum age constraints for the stem node of their assigned clade, which ensures conservative dating by using minimum ages provided by fossil evidence (Doyle and Donoghue, 1993; Renner, 2005; Benton and Donoghue, 2007). The shape of the prior distribution for the fossil constraint influences the age estimation and should be selected to reflect the current biological understanding of the fossil and the group it is assigned to (Benton and Donoghue, 2007; Ho and Phillips, 2009). Log-normally- or exponentially-distributed priors place the highest probability on ages just older than the fossil constraint and lower probabilities with increasing distance to the constraint. This is seen as biologically realistic (Renner, 2005; Benton and Donoghue, 2007; Crisp et al., 2010; Bell et al., 2010; Smith et al., 2010). Uniform priors require fewer parameters to be defined and may therefore be preferable in the absence of detailed palaeontological information provided by a fossil sequence (Ho and Phillips, 2009; Clarke et al., 2011). I decided to use uniformly- and gamma-distributed priors for fossil calibrations in my multi-fossil divergence dating of the Araceae (Chapter 2). Age estimates with these two shapes of prior distributions are very similar (Chapter 2, Supplementary Table 4).

The shapes of posterior distributions of the constrained nodes permit evaluating the influence of the prior constraints on the estimated ages. In my Araceae dataset, the posterior distributions (Chapter 2, Supplementary Figure 3) obtained for three of the constrained nodes were substantially shaped by their priors (*Nitophyllites zaisanicus*, *Araciphyllites tertiarius*, and *Petrocardium cerrejonense*). On the other hand, *Lasioideaecidites hessei*, *Limnobiophyllum scutatum*, and *Montrichardia aquatica* hardly affected the posterior distribution of the nodes to which they were assigned. It seems that these fossils are much younger than the nodes they have been assigned to and that they therefore have little influence on the divergence dating. In general, one expects to find fossils that are younger than the stem node of the clade they are assigned to.

In a Bayesian framework, the ways in which substitution rates can change across a phylogeny in a relaxed clock model are determined by prior distributions. With the software TreeTime (Himmelmann and Metzler, 2009), rate changes can be applied according to the compound Poisson process, the Dirichlet model, an uncorrelated exponential distribution, or an uncorrelated log-normal distribution. In Chapter 2, all four relaxed clock models were used, as well as the uncorrelated log-normal in BEAST. Age estimates differed especially in the basal-most nodes, but were relatively consistent in distal nodes (Chapter 2, Supplementary Table 4). TreeTime differs from BEAST in using no tree prior, but instead assuming a uniform prior for all combinations of branch lengths, which is conditioned on the exponentially distributed age of the root and the additional priors specified by the user for time calibration. This may be the reason for the generally older root ages and the differences in age estimates in TreeTime.

For my study of *Alocasia* and its outgroup, I used a single Eocene fossil, *Caladiosoma messelense* (Wilde et al., 2005), with a standard distributed prior shape on the constrained node, such that 90% of the permitted ages fell into a range of 47–47.5 Ma, the age of the fossil. This narrow range is justified by the well-constrained dating of the Messel Formation (V. Wilde, Senkenberg Museum, Frankfurt, Germany, pers. comm., 2009). This fossil assignment, however, turned out to be problematic once it became clear that *Alocasia hypnosa* did not group with the rest of *Alocasia* (Chapter 3, Figure 3). I then resorted to apply the *Caladiosoma messelense* to all 15 possible topologies among major clade in my dataset (Chapter 3, Supplementary Table 2). The *Caladiosoma messelense* fossil was not included in the Araceae family dating, thus allowing cross-validation of the resulting ages among my *Alocasia* study and my family-level study; the age of the corresponding node in the multi-fossil calibrated analysis of Chapter 2 was an estimated 45.68 Ma (95% confidence interval: 35.09–55.26 Ma) — very close to the actual age of the fossil (47–47.5 Ma).

Model complexity The use of parameter-intensive methods always carries the danger of over-parametrization. In Chapter 2, I compared two substitution models with different complexity. The software Modeltest (Posada and Crandall, 1998) suggested a complex model with TPM1uf+Γ for the non-coding region and GTR+Γ for the coding region, with the third codon position analysed separately. Age estimated under these complex models were very similar to those obtained with the much simpler JC+Γ model (only diverging 4.1% on average; Chapter 2, Supplementary Table 4), but calculation times were four times longer under the complex models. Only one model (HKY+Γ; suggested by Modeltest) was used in Chapter 3.

Rate heterogeneity The relaxed clock method used in the dating of the Araceae family phylogeny in Chapter 2 allowed changes in DNA substitution rates between lineages (Chapter 2, Supplementary Figure 1). They ranged from $1.23E^{-4}$ to $2.19E^{-3}$ substitutions per site per million years and showed a strongly skewed distribution, with only few lineages reaching high values (Chapter 2, Supplementary Figure 1, inserted graphic). Seven of the ten highest rates occurred in the free-floating or submerged Lemnoideae, *Pistia*, and Cryptocoryneae (Chapter 2, Supplementary Figure 1, nodes 2, 6, 7, 9, 10, 95, and 97). DNA substitution rate variations have been suggested to correlate with body size, population dynamics, and lifestyle (Bromham, 2009). Smith and Donoghue (2008), for example, found higher rates in herbaceous compared to woody plants in five major clades across the angiosperms. Several factors may play a role in the higher rates of strongly water-associated Araceae, for example, a higher exposure to UV light due to the free-floating habit, small body size, short generation times, and often clonal reproduction (Lemon et al., 2001).

Estimated divergence times According to the age estimates in Chapter 2, the Araceae family diverged from the rest of the Alismatales in the Early Cretaceous, when the breakup of Pangea was almost complete. This relatively old age of the Araceae is supported by two fossil infructescences with *in situ* pollen from the late Aptian–early Albian of Portugal (Friis et al., 2010) and one fossil leaf of similar age from the Crato Formation in Brazil (Clement Coiffard, Berliner Naturkunde Museum, pers. comm., May 2011). All three fossils demonstrate that a certain morphological and geographical diversity already existed in the early evolution of the Araceae. Fossils that can be assigned to subfamily level are known from the Late Cretaceous (Orontioideae, Bogner et al., 2005, 2007; Lasioideae, Hofmann and Zetter, 2010; Lemnoideae, Kvaček, 1995; Stockey et al., 1997; Chapter 2, Supplementary Table 2). The age estimates, however, showed the emergence of most subfamilies much earlier than their first known fossil evidence (Chapter 2, Supplementary Table 4).

The age estimates for the divergence of *Alocasia* (Chapter 3) inferred a close correlation between the evolution of the genus and the climatic history of the Malesian region. *Alocasia* split from its sister clade at the end of the Oligocene and started to diversify in the middle Miocene (Chapter 3, Figure 4). The collision between the Australian and Eurasian plates started in the late Oligocene, about 25 Ma ago (Hall, 2002, 2009) and led to the emergence of islands and dispersal routes. Pollen records from the middle Miocene indicate a warm and humid climate with rainforest expansion onto these newly forming islands (Morley, 1998), and groups adapted to the rainforest understory, such as *Alocasia*, could have plausibly spread and diversified.

Biogeographical Analyses

Model comparison The parsimony-based Bayes-DIVA approach and the likelihood-based DEC approach (without constraining dispersal probabilities) to the Alocasia data (Chapter 3) yielded only a few differences in the results: Two ingroup nodes (Chapter 3, Supplementary Table 3, nodes 26 and 41) differ in the most probable scenario found with DEC compared to the Bayes-DIVA results. Neither result was well supported. Another affected outgroup node (node 24), however, illustrates the differences between the two methods; Bayes-DIVA reconstructs a biologically implausible ancestral area for this node of Asia plus Australia (AF), while the DEC approach permits multiple range shifts along the branches and reconstructs Borneo as the origin of the Australian lineage, indicating a later dispersal to Australia, although it is not directly connected.

For the biogeographic reconstruction of the Araceae family-level dataset, I used only the DEC approach, which allows incorporation of dispersal constraints such as plausibly result from changes in continent connectivity and climate history since the Early Cretaceous. So far, this approach has been used in a limited number of studies as listed in Table 1 of Chapter 2.

DEC model complexity Although the inclusion of dispersal probabilities in the DEC approach has merits, unnecessary complexity decreases the power of any model. This issue, namely testing for possible over-parametrization of models, is rarely considered in biogeographic work, a fact also bemoaned by Pirie et al. (2012). In a likelihood framework, comparing DEC model fit is not possible, because the different models are not nested (they differ from each other in more than one parameter). In my work, I compared two DEC models, one with three time-slices and one with four (meaning the matrices of dispersal probabilities had three or four time bins, delimited in millions of years before present; Chapter 2, Supplementary Table 3). In the absence of a statistically valid method for assessing which of the two models might fit the data better, I used the overall likelihood score as given by the Lagrange software as a proxy. The simpler model with three time-slices had a higher likelihood and was therefore preferred. Mao et al. (2012), the only other study to have compared the fit of DEC time-slice models, compared models using five to eight time-slices for a Cupressaceae data set with 126 species, and 16 fossil constraints (compared to the 145 species, and 7 fossil constraints in my dataset) and found that the most complex model (with eight time-slices) had a better likelihood than the simpler models. It is unclear why the Araceae data were better described by a simpler model than the Cupressaceae data.

Incorporation of fossil ranges The incorporation of fossil ranges directly into the computer-based ancestral area reconstructions revealed additional transitions between North America and Eurasia of the Orontioideae in the Late Cretaceous and yielded a wider ancestral range of the ancestor of *Anthurium* and the Lasioideae subfamily (Chapter 2, Figures 3 and S3). It also influenced the deepest nodes in the Araceae that had ambiguous reconstructions and were sensitive to model changes (Chapter 3, nodes 1 and 2). Two other studies have included fossil ranges in ancestral area reconstructions for the entire families, viz Simaroubaceae (Clayton et al., 2009) and Cupressaceae (Mao et al., 2012). Both studies integrated fossils as if they represented living lineages; this was done by given the fossils branch lengths proportional to their age (e.g., a fossil that lived 60 Ma ago would have a branch length from 60 Ma ago to the present). The idea was to simulate remnant distributions ("paleoendemics"). When I compared this approach to one in which I included Araceae fossils by giving them short branches (simulating that the respective fossil lineage went extinct soon after the time horizon in which it was found), I found that fossils on shorter branches resulted in a stronger influence of fossil ranges on the overall reconstruction. To my mind, the approach using shorter branches is more realistic than including fossil on long branches (Chapter 3, Supplementary Table 5).

Overall, ancestral area reconstructions obtained when fossil ranges where included in the analyses were more plausible than those without fossil ranges. This is not a trivial result because only in a quantitative (computer-based) analysis is it possible for fossil ranges to influence results (here areas) at distant nodes in the phylogenetic tree. The approach is likely to become widely used in future biogeographic work on clades that are relatively old and have a good fossil record.

Extinction and range shifts Most subfamilies in the Araceae, except for the Aroideae, have relatively long stem lineages. Modeling work on the shapes of phylogenetic trees has shown that long stems leading to clusters of short branches can indicate mass extinctions (Crisp and Cook, 2009). The Lasioideae have an exceptional long stem lineage (Chapter 2, Figure 3; stem age 90 Ma, crown age 26 Ma). Fossils of this group are known from the Late Cretaceous of Siberia and the Eocene of Canada (Smith and Stockey, 2003; Hofmann and Zetter, 2010), but today they occur only in tropical latitudes, which indicates that they experienced extinction in the northern hemisphere, probably when climates changed in the Oligocene. Extinction in Eurasia and North America and survival in tropical Southeast Asia, South America, or Africa seems to be the prevailing pattern in Araceae, occurring in all species-rich subfamilies (Aroideae, Lasioideae, Monsteroideae, and Pothoideae). Similar effects of the Oligocene climate cooling and the Quaternary ice ages have been documented for many plant groups.

Reconstructed areas and dispersal routes The origin of the Araceae family dates to the breakup of Pangea with biogeographic reconstructions so far ambiguous between a Laurasian or a water-associated origin of the family's earliest branches (Chapter 2, Supplementary Table 5). Early Araceae that occupied wet habitats fits with the ecology of and fossils associated with early-diverging clades in the family (Kvaček, 1995; Bogner et al., 2007). Of the first three subfamilies, the Lemnoideae are free-floating and the Orontioideae occur in swampy habitats. The only species of the Gymnostachydoideae occurs in Australia and is probably a remnant of a formerly wider distribution; it could have reached Australia during the last 100 million years along several routes. From its Laurasian origin the Araceae took several routes to reach the pantropical distribution observed today. Not all living Araceae rely on megathermal conditions (exceptions are Orontioideae, many Lemnoideae, and some Aroideae like *Arisaema*, *Calla*, and *Peltandra*), but most clades do so. Possible dispersal routes for megathermal plants appeared and disappeared since the breakup of Gondwana with changing climates and continental connectivity. During the Paleocene and Eocene, warm climates allowed dispersal across Antarctica, which was still connected to South America and Australia, as well as dispersal across the North Atlantic land bridge connecting North America and Eurasia (Morley, 2003). With the climate cooling in the Oligocene this was no longer possible, but plate movement facilitated dispersal from Australia and Africa to Asia, and connected North with South America (Coates et al., 1992; Hall, 2002, 2009; Cody et al., 2010).

The pantropical Lasioideae, Monsteroideae, and Pothoideae originated and diversified in the northern hemisphere. Dispersal to tropical South America, Southeast Asia, Africa, and Australia occurred almost exclusively in the Neogene, the only exception being the lineage that leads to *Anthurium*, which existed in South America already in the Paleocene (Herrera et al., 2008). In the Aroideae, however, transitions to South America and Southeast Asia occurred several times during the Paleogene, when warm climates allowed dispersal across the North Atlantic land bridge followed by dispersal to South America. In the Neogene many lineages moved from Asia to Southeast Asia, colonized the Malaysian Archipelago, and some even dispersed to Australia. Transitions from Asia to Africa in the Aroideae, as well as in the lineage leading to the Zamioculcadoideae, happened either before the Eocene or after the Oligocene.

Even though the Araceae do not seem to be adapted for long-distance dispersal, not all disjunctions can be explained by vicariance. This applies to the disjunctions between South America and Asia in the Lasioideae, Monsteroideae (e.g., *Monstera* and *Spathiphyllum*), and Aroideae (*Homalomena* and *Philodendron*) subfamilies, as well as the transition to islands distant from continents like Madagascar or the Seychelles, and all genera crossing the ocean expanses of the Malay Archipelago. All genera today occurring on Australia reached the continent in the Neogene from Southeast Asia, involving island hopping; the only exception may be *Gymnostachys*, which is old enough to have reached Australia via Antarctica before the complete breakup of Gondwana.

The number of dispersal events in the Araceae is small compared to other families for which a similar biogeographic analyses have been undertaken. In Cucurbitaceae, for example Schaefer et al. (2009) count at least 43 dispersal events across major sea barriers. However, my sampling of mostly one species per genus provides only a relatively coarse view on the biogeography of Araceae (Chapter 2) and overlooks dispersal events occurring within species-rich genera, especially the ones distributed in the Southeast Asian region. An example is provided by the genus *Alocasia*, analyzed with dense species sampling in Chapter 3. The dense sampling reveals at least 10 dispersal events across ocean expanses.

Before reaching the Malay Archipelago, *Alocasia* diverged from its sister taxon *Colocasia gigantea* on the Asian mainland at the end of the Oligocene. The main diversification of *Alocasia* then took place at the end of the Miocene on Borneo, from where it dispersed to the Philippines at least four times and back to the Asian mainland at least six times. Sulawesi and New Guinea were not reached until approximately 5–7 Ma ago, which is in concordance with the plate tectonic interpretations of Hall et al. (2008) and Hall (2009). A similar pattern of genera colonizing the eastern part Malay Archipelago not earlier than 10 Ma ago was found in Aglaieae (Meliaceae; Muellner et al., 2008), *Pseuduvaria* (Annonaceae; Su and Saunders, 2009) and *Begonia* (Begoniaceae; Thomas et al., 2011).

A nice result of the work on *Alocasia* is that it revealed the origin of the two widely cultivated *Alocasia* species, *A. macrorrhizos* (giant taro) and *A. cucullata* (Chinese taro). *Alocasia macrorrhizos* is genetically very closely related to the Philippine endemic *A. portei* (Chapter 2, Figure 3), which has been suspected based on morphological features by Hay (1999); its geographic origin thus lies in the Philippines. *Alocasia cucullata*, which is closely related to the Asian species *A. odora* and *A. navicularis*, originated on the Asian mainland.

General conclusion

Careful choice of methods and comparison of different quantitative approaches, many developed over the last years, allowed me to construct the biogeographic history of the Araceae family and of the genus *Alocasia* across the Malay Archipelago. Araceae originated after the breakup of Gondwana and probably initially occupied wet habitats. Many subfamilies evolved in the Late Cretaceous on the Laurasian continent and reached their current pantropical distribution by dispersal in the Paleocene, Eocene, and Neogene. Extinction in the temperate region during the Oligocene climate cooling must have been extensive. The *Alocasia* clade originated on the Asian mainland in the late Oligocene and dispersed into the Malay Archipelago in the Miocene according to the geologic and climatic development of the region. Hybridization events with chloroplast capture may have played a major role in the evolution of *Alocasia*.

A

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B

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C

Posters

Phylogeny and biogeography of *Alocasia (Araceae)*, and a DNA-based identification service

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Introduction

Alocasia is distributed in the whole South East Asian Region with a probable origin on the Eurasian mainland. A dated phylogeny permits correlating the diversification of lineages with geologic and climatic changes of the past. Here we adress the timing of the main diversification events is *Alocasia* and ultimately the radiations on different islands.

Information about *Alocasia* (Schott) G. Don

~75 species with a center of diversity on Borneo ~36 species (P. Boyce, pers. com., May 2009). High proportions of endemics: Philippines 13 of 14 species, Papuasia 11 of 12. Many popular ornamental plants (see photos).

Fig.1: Distribution map of Alocasia
Mayo, Bogner & Boyce 1997. The Genera of Araceae

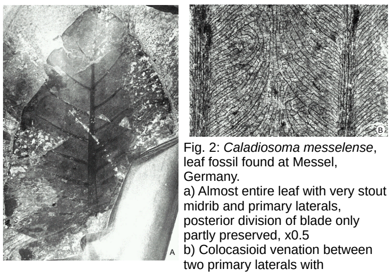


Fig. 2: *Caladiosoma messelense*, leaf fossil found at Messel, Germany.
a) Almost entire leaf with very stout midrib and primary laterals, posterior division of blade only partly preserved, x0.5
b) Colocasioid venation between two primary laterals with interprimary collective vein(s), x4 (Wilde et al. 2005).
Fossil age: ~47-47.5 Ma (V. Wilde, pers. com., Jan. 2009) used as calibration for the molecular clock (arrow in chronogram).

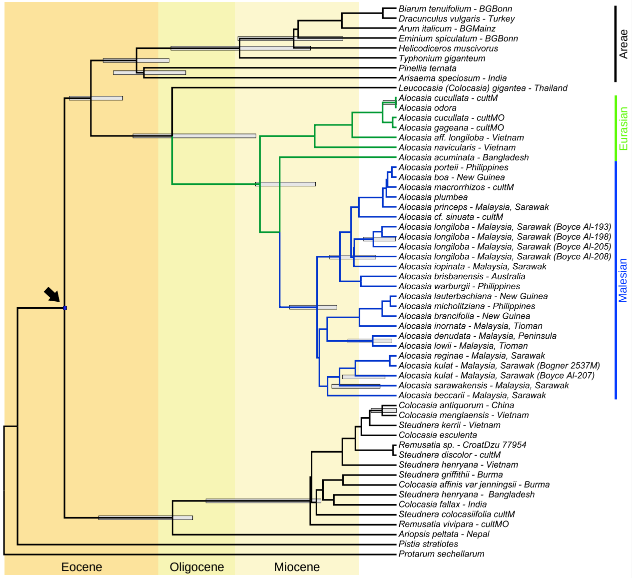


Fig. 3: Chronogram from a strict molecular clock, GTR + Gamma Model, bars are only on supported branches and show 95% confidence interval.
Phylogeny based on 3271bp (trnL intron and spacer, trnK intron and matK gene). Tree rooted following the family phylogeny of Cusimano et al. (in prep.).

For more information see Cusimano, Mayo & Bogner (abstract and poster at this conference): **Relationships within the Araceae: Comparison of morphological patterns with molecular phylogenies.**

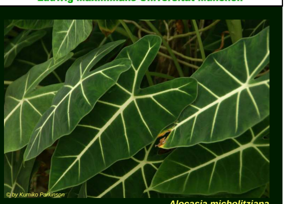
Results

Alocasia is monophyletic and together with *Leucocasia* Schott located outside of the other Colocasieae and sister to the Areae clade. Some species have yet to be revised and the identity of vouchers clarified. The colonization of the Malesian islands from the Eurasian mainland can be dated to the middle to early Miocene.

DNA-based identification

Identifying species by comparing their DNA to reference sequences requires only small leaf fragments. This method might be interesting for identification of plants of unknown species and origin. We are offering the identification of such plant material, to see if there is demand for this service.

Refernces:
1) V. Wilde, Z. Kvacek and J. Bogner. 2005. Fossil leaves of the Araceae from the European Eocene and notes on other aroid fossils. *International Journal of Plant Science.* 166:157–183.
2) N. Cusimano, J. Bogner, S.J. Mayo, R.C. Keating, P.C. Boyce, S.Y. Wong, W. Hetterscheid, M. Hesse and J.C. French. Relationships within the Araceae: comparison of morphological patterns with molecular phylogenies. *in prep.*
3) All photos taken by Peter Boyce, except for the upper right one, which was taken by Kumiko Parkinson (kumikokp@gmail.com).



Alocasia micholitziana

Alocasia scabriuscula

Alocasia sinuata

Alocasia longiloba ‚watsoniana'

Alocasia reginae

Alocasia reversa

Alocasia chaii

Alocasia longiloba ‚lowii'

Alocasia princeps

Alocasia princeps

Alocasia reversa

Alocasia reginula

Biogeography of *Alocasia* (Araceae): colonization of the Malay Archipelago

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Introduction

Alocasia is distributed in South East Asia with an origin on the Eurasian mainland. We present here a dated phylogeny of the genus with sufficient outgroup sampling to infer the dispersal and diverging times. The goal is to reconstruct the colonization of the Malay Archipelago and to relate dispersal events to climate changes in the past.

Expansion of rainforest from the middle Miocene on enabled the shade-loving *Alocasia* to increase ist range and to diversify as it reached the different islands.

Information about *Alocasia* (Schott) G. Don

- 100+ species (85 described): Borneo (45+), Philippines (20+), New Guinea (12+), Sulawesi (9+), Eurasia (8), Java & Sumatra (5), Australia (1)
- mostly lowland rain forest understorey, rarely in highlands or on exposed sites
- many limestone species
- almost all species endemic to their island or region
- fruit-fly pollinated (*Colocasiomyia*), bird dispersed
- many ornamental species

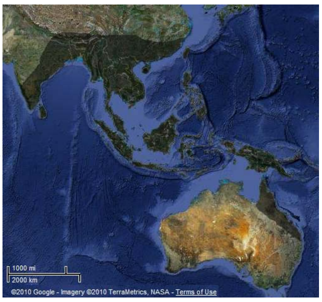
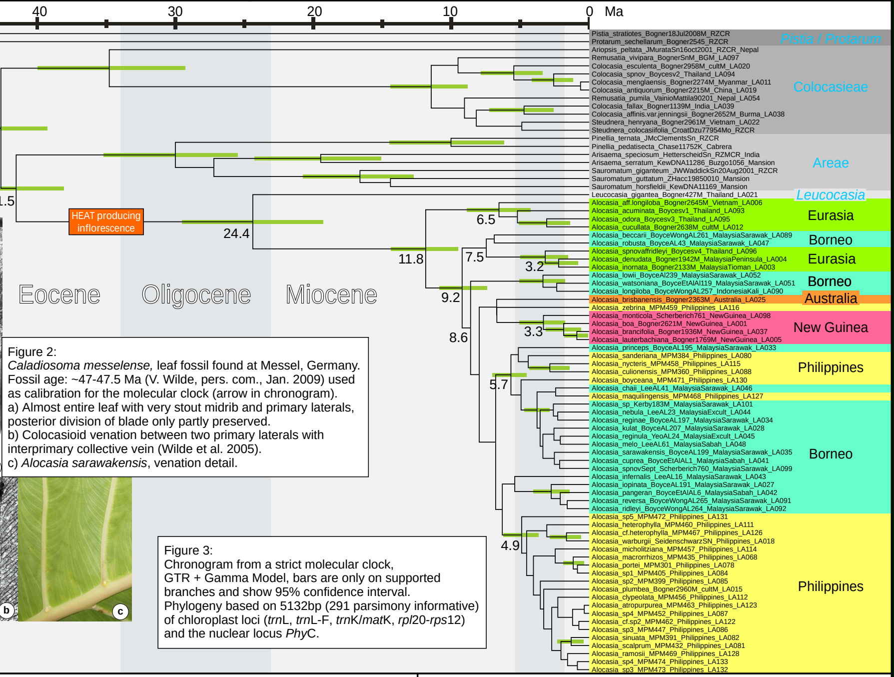


Figure 1: Distribution map of *Alocasia*.



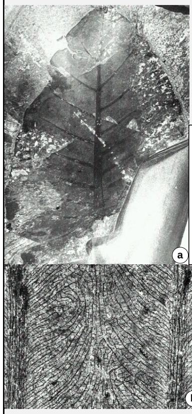


Figure 2:
Caladiosoma messelense, leaf fossil found at Messel, Germany. Fossil age: ~47-47.5 Ma (V. Wilde, pers. com., Jan. 2009) used as calibration for the molecular clock (arrow in chronogram).
a) Almost entire leaf with very stout midrib and primary laterals, posterior division of blade only partly preserved.
b) Colocasioid venation between two primary laterals with interprimary collective vein (Wilde et al. 2005).
c) *Alocasia sarawakensis*, venation detail.

Figure 3:
Chronogram from a strict molecular clock, GTR + Gamma Model, bars are only on supported branches and show 95% confidence interval.
Phylogeny based on 5132bp (291 parsimony informative) of chloroplast loci (*trnL*, *trnL*-F, *trnK*/*matK*, *rpl20*-*rps12*) and the nuclear locus *PhyC*.

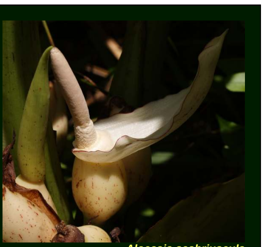
Results

- *Alocasia* evolved in the middle Miocene and dispersed into the Malesian Archipelago in the late Miocene, following the expanding rainforest.
- Main diversification occurred in the Pliocene and Pleistocene.
- There have been multiple colonizations between Eurasia, Borneo, and the Philippines, but probably only one dispersal event to New Guinea.
- New Guinea was colonized from the Philippines.

Other interesting findings

- The data reveal that *A. macrorrhizos*, long cultivated because of edible tubers and leaves, originates from the Philippines.
- Only 11 of the 450 families of flowering plants produce heat. Our data suggest that *Alocasia* and its sistergroup ancestrally produced heat in their inflorescences. This trait is an interesting synapomorphy.

References:
1) V. Wilde, Z. Kvacek and J. Bogner. 2005. Fossil leaves of the Araceae from the European Eocene and notes on other aroid fossils. *International Journal of Plant Science.* 166:157–183.
2) All photos taken by Peter Boyce.



Alocasia scabriuscula

Alocasia cuprea

Alocasia longiloba ‚lowii'

Alocasia robusta

Alocasia venusta

Alocasia longiloba ‚watsoniana'

Alocasia infernalis

Alocasia robusta

Alocasia chaii