Phylogeny and classification of the Australasian and Indomalayan mimosoid legumes *Archidendron* and *Archidendropsis* (Leguminosae, subfamily Caesalpinioideae, mimosoid clade)

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Abstract

The morphologically variable genus *Archidendron* is the second largest mimosoid legume genus from the Indomalayan-Australasian region, yet it has not been well represented in phylogenetic studies. Phylogenies that have included multiple representatives of *Archidendron* suggest it may not be monophyletic, and the same applies to *Archidendropsis*, another understudied genus of the Archidendron clade. The most comprehensive phylogeny of *Archidendron* and *Archidendropsis* to date is presented, based on four nuclear markers (ITS, ETS, SHMT and RBPCO). Exemplars from all genera of the wider Archidendron clade are sampled, including representatives of all series within *Archidendron* and the two subgenera of *Archidendropsis*. Our results confirm that *Archidendron* and *Archidendropsis* are not monophyletic. Within *Archidendron*, only one series (ser. *Ptenopae*) is resolved as monophyletic and species of *Archidendron* are divided into two primarily geographic lineages. One clade is distributed in western Malesia and mainland Asia and includes most representatives of series *Clypeariae*, while the other is mostly restricted to eastern Malesia and Australia and includes representatives of the seven other series plus two samples of series *Clypeariae*. No taxonomic changes are made for *Archidendron* due to the high level of topological uncertainty and the lack of discrete macromorphological characters separating these two lineages. Each of the two subgenera of *Archidendropsis* is monophyletic but they are not closely related. A new genus endemic to Queensland (Australia), *Heliodendron* Gill.K. Br. & Bayly, gen. nov., is described for the former *Archidendropsis* subg.

Keywords
Fabaceae, ingoid clade, legumes, low copy nuclear gene, Malesia, phylogeny, targeted amplicon sequencing

Introduction

The classification of mimosoid legumes has been significantly transformed in the past 20 years since the first comprehensive molecular phylogeny of the then subfamily Mimosoideae (Luckow et al. 2003). Understanding of relationships within the mimosoid legumes has improved through studies at generic, regional, alliance, subfamilial and familial levels (see references in Legume Phylogeny Working Group 2017; Koenen et al. 2020; Ringelberg et al. 2022). In the comprehensive phylogeny and revision of the legume family (Leguminosae or Fabaceae), the mimosoid legumes formed a clade nested within the re-circumscribed subfamily Caesalpinioideae (Legume Phylogeny Working Group 2017). Recent phylogenomic data have sufficiently enhanced resolution to enable recognition of several clades within subfamily Caesalpinioideae, including the mimosoid, core mimosoid and ingoid clades (Koenen et al. 2020; Ringelberg et al. 2022). However, within these clades some large genera, such as Archidendron F. Muell. and allies have remained under-studied relative to Acacia Mill. s.l. and many Neotropical ingoid genera and groups (e.g. Murphy et al. 2010; de Souza et al. 2013; Iganci et al. 2016; Miller et al. 2017; Ferm et al. 2019; Comben et al. 2020).

The two largest mimosoid genera from the Indomalayan-Australasian region are Acacia and Archidendron. These are placed in the Archidendron clade (sensu Koenen et al. 2020), along with Archidendropsis I.C. Nielsen, Falcataria (I.C. Nielsen) Barneby & J.W. Grimes, Pararchidendron I.C. Nielsen, Paraserianthes I.C. Nielsen, Serianthes Benth. and Wallaceodendron Koord. The Archidendron clade is biogeographically distinct within the mimosoid legumes, being primarily restricted to the Indomalayan and Australasian regions, and has been given several names over the years to reflect this: the Australian & SE Asian Ingeae clade (Brown et al. 2008) and the Australo-Malesian mimosoids (Brown et al. 2011). Within the Archidendron clade, Pararchidendron, Paraserianthes and Wallaceodendron are monotypic, and three of the other five genera (Acacia s.s., Falcataria, and Serianthes) are well documented as monophyletic based on morphological and genetic data (Chappill and Maslin 1995; Miller and Bayer 2001; Luckow et al. 2003; Brown et al. 2008, 2011; Murphy et al. 2010; Demeulenaere et al. 2022; Ringelberg et al. 2022). However, Archidendron has been suggested to be paraphyletic (Brown et al. 2008, 2011; Iganci et al. 2016; Demeulenaere et al. 2022; Ringelberg et al. 2022), as has Archidendropsis (Demeulenaere et al. 2022; Ringelberg et al. 2022).

Archidendron is the second largest genus in this clade after Acacia, with 99 described species and an additional 20 putative species that are poorly known due
Phylogeny of Australasian mimosoid legumes *Archidendron* and *Archidendropsis*

Archidendron and Archidendropsis

Archidendron and Archidendropsis are small to medium-sized trees found in lowland and montane tropical and subtropical rainforests of the Australo-Malesian and Pacific regions, distributed from Kerala (southern India) and Sri Lanka in the west, to the Solomon Islands in the east; and from Taiwan and the Ryukyu Islands in the north, to Australia in the south (Fig. 1; Nielsen et al. 1984b, 1984a). In the 1970s and 1980s, an extensive revision of the Australo-Malesian and Pacific Ingeae was undertaken (Nielsen 1979, 1981, 1982; Nielsen et al. 1983b, 1983a, 1984b) and *Archidendron* was expanded based on evidence from wood, pollen, seed and inflorescence characteristics to include species previously referred by Kostermans (1954) to the genera *Abarema* Pittier, *Cylindrokelupha* Kosterm., *Morolobium* Kosterm., *Paralbizzia* Kosterm., *Zygia* P. Browne, and by Bentham (1875) to *Pithecellobium* sect. *Cympaea* sensu Benth. (Baretta-Kuipers 1981; Nielsen et al. 1984b; Nielsen 1992). *Archidendron* now includes unarmed trees or shrubs with bipinnate leaves, mostly opposite leaflets, extrafloral nectaries, and wood anatomy of strictly uniseriate rays and abundant parenchyma with a banded distribution (Nielsen et al. 1984b).

*Archidendron* is morphologically variable especially in leaf, inflorescence, flower, and pod characteristics, and has been divided into eight series (Nielsen et al. 1984b): *Cympaea* (Benth.) I.C. Nielsen, *Archidendron*, *Calycinae* I.C. Nielsen, *Bellae* I.C. Nielsen, *Ptenopae* I.C. Nielsen, *Pendulosae* (Mohlenbr.) I.C. Nielsen, *Stipulatae* (Mohlenbr.) I.C. Nielsen and *Morolobiae* (Kosterm.) I.C. Nielsen. The largest series, *Cympaea* (ca. 51 species) is distributed in mainland southeast Asia, western Malesia, and the Philippines, with only a few species found further east (Fig. 1A). This series is well defined by the absence of stipules and flowers that generally have one carpel per ovary that is often stipitate (Nielsen et al. 1984b). The second largest series, *Archidendron* (ca. 15 species), is found in eastern Malesia and Australia and is defined by the presence of stipules and stipular glands. Four of the series are largely confined to the island of New Guinea (Nielsen et al. 1984b): series *Cympaea* (3 species) with strongly ribbed inflated calyces, cauliflorous racemes and sessile ovaries; series *Bellae* (4 species) with large woody pods without overgrown seeds and cauliflorous paniculate inflorescences; series *Ptenopae* (2 species), which is defined by the presence of two-winged rachises and pinnae; series *Pendulosae* (3 species) have inflorescences with lax racemes (Nielsen et al. 1984a). Series *Stipulatae* (ca. 14 species) are found in New Guinea, the Moluccas, and Queensland (Australia) and have floral bracts with extra floral nectaries, stipular glands and cauliflorous branched racemes (Nielsen et al. 1984b). The three species of series *Morolobiae* have unifoliolate pinnae, and racemose inflorescences with flowers with single, sessile ovaries, and are disjunctly distributed: *A. monopterum* (Kosterm.) I.C. Nielsen in Halmahera (North Maluku Islands, Indonesia), *A. whitei* I.C. Nielsen in northern Queensland (Australia) and *A. muellerianum* (Maiden & R.T. Baker) I.C. Nielsen in northern New South Wales (Australia) (Nielsen et al. 1984b).

Prior to resolution of the Archidendron clade, the genus *Archidendron* was suggested to be related to taxa of the Inga-alliance (Barneby and Grimes 1996; Lewis and Rico Arce 2005) or to other Old World genera, such as *Archidendropsis*, *Falcatoria*, *Parach dendron*, and...
Paraserianthes and Serianthes (Baretta-Kuipers 1981; Nielsen et al. 1984a; Nielsen 1992). *Archidendron* has not been well represented in molecular phylogenies to date with only ten of the 99 species and four of the eight series (*Archidendron*, *Clypeariae*, *Morolobiae* and *Ptenopae*) included in any one study. In all studies, samples of series *Clypeariae* are placed distantly from the other series (Brown et al. 2008, 2011; Iganci et al. 2016; Koenen et al. 2020; Demeulenaere et al. 2022; Ringelberg et al. 2022). Only two studies have included representatives of each of the subgenera and in both, *Archidendropsis* is not resolved as monophyletic (Demeulenaere et al. 2022; Ringelberg et al. 2022).

The genus *Archidendropsis* includes 14 species from New Caledonia, the Solomon Islands, New Britain, Papua New Guinea and Australia (Fig. 1B), with all species endemic to their respective region (Nielsen et al. 1983a). Species of *Archidendropsis* have winged, thin-walled seeds lacking a pleurogram (a mark or depression on both sides of the seed coat; Rodrigues-Junior et al. 2021) and are placed in two subgenera based on pollen and inflorescence characteristics. Species of subgenus *Basaltica* I.C. Nielsen are restricted to Australia, have smaller polyads (55–60 μm) and globular inflorescences, while species of subgenus *Archidendropsis* are not found in Australia, have larger polyads (80–120 μm) and flowers arranged in spicate racemes. Like *Archidendron*, *Archidendropsis* has been poorly represented in molecular phylogenies with only one or two of the 14 species included in any one study (Brown et al. 2008, 2011; Ferm et al. 2019; Koenen et al. 2020; Demeulenaere et al. 2022; Ringelberg et al. 2022). Only two studies have included representatives of each of the subgenera and in both, *Archidendropsis* is not resolved as monophyletic (Demeulenaere et al. 2022; Ringelberg et al. 2022).
This study aims to test the monophyly of the genera *Archidendron* and *Archidendropsis* and investigate phylogenetic relationships within the large genus *Archidendron* to test the monophyly of its infrageneric series.

**Materials and methods**

**Taxon sampling and DNA isolation**

A total of 87 accessions were sampled, representing 43 species of *Archidendron* (68 accesses), five species of *Archidendropsis* (six accessions) and nine species (11 accessions) of the other genera in the Archidendron clade; two species of Old World *Albizia* Durazz. were included as outgroups (Table 1). In total 43% of the species of *Archidendron* were sampled including representatives of all eight series. Both subgenera of *Archidendropsis* were sampled covering 36% of species in the genus. Samples were collected in the field and from herbarium specimens sourced from AAU, BISH, BRI, CANB, CNS, KEP, KUN, L, NY, MEL and MELU (herbarium codes as per Thiers, updated continuously).

Total genomic DNA (gDNA) was extracted following the CTAB method of Doyle and Doyle (1987) with modifications as per Shepherd and McLay (2011). Isolated gDNA was quantified with a NanoDrop 2000 (ThermoScientific) spectrophotometer and cleaned with a 2.4 M sodium acetate wash. Recalcitrant herbarium material that failed using the CTAB method was extracted using the AccuPrep Stool genomic DNA extraction kit (Bioneer) using the manufacturer’s protocol with some modifications suggested by Schuster (pers. comm.). Only 30 mg of leaf material was used instead of the recommended 100–200 mg. A total of 600 μl of stool lysis buffer (SL) was added to the extraction tube instead of 400 μl, the incubation step was increased to one hour in total, centrifugation was done for 10 minutes at step five, and to maintain equal volumes, 600 μl of binding buffer was added. Two consecutive washes were performed using buffer 1 (W1). The final elution was done by adding 160 μl total elution buffer in two steps (first 60 μl, and then 100 μl) instead of a single elution with 200 μl.

**Marker selection, primer design and library preparation**

Eight nuclear markers (low copy genes: *AIGP*, *CYB6*, *Eif3E*, *SHMT*, *RBPCO*, *UDPG*; nrDNA: *ITS*, *ETS*) and four chloroplast DNA intergenic spacer regions (*trnK–matK*, *trnV–ndhC*, *psbD–trnT*, *trnL–rpl32*) were assessed for variability between nine individuals spanning the series of *Archidendron* using Sanger sequencing.

PCR reagents, primers and cycling conditions are described in Suppl. material 1 (Johnson and Soltis 1994; Sun et al. 1994; Käss and Wink 1997; Baldwin and Markos 1998; Miller and Bayer 2001; Ariati et al. 2006; Choi et al. 2006; Shaw et al. 2007; Li et al. 2008). PCR products were visualised on a 1.5% agarose gel with Easy ladder I (Bioline) and cleaned with ExoSAP-IT (USB) as per the manufacturer’s protocol. The purified amplicons were sequenced on an AB3730xl sequencer (Thermo Scientific) at
Table 1. Linked data table of specimens sampled for phylogeny. Specimen accession number linking herbarium specimen to sample ID, taxon name with authorities, locality information and geocode (where available) as provided on the specimen/database. GenBank numbers are provided for each marker and where multiple alleles were identified for a specimen, the two GenBank numbers are separated by a semi colon. If the marker was not successfully sequenced for a particular specimen, then the GenBank field is left blank.

<table>
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<tr>
<th>Preserved specimen</th>
<th>Associated sequences</th>
<th>Taxon name/MOTU</th>
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<th>GPS Coordinates</th>
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<td>0.7km north of Playford Highway on Snug Bay Rd, Kangaroo Island, South Australia</td>
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<td>Alva, NE of Ayr, Queensland, Australia</td>
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### Phylogeny of Australasian mimosoid legumes

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<td>ON101525</td>
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<td>JA95</td>
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<td>OM984594</td>
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<td>Mt Cooinda, West Foresta</td>
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<td>OM013685</td>
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<td>Pa Daili area, Sarawak</td>
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<td>OM287022</td>
<td>OM013683</td>
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<td>Bandy Creek Road, 9 km S of Airlie Beach, Queensland, Australia</td>
<td>14°43'15.38''E, 150°49'40''S</td>
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**Note:** The above table provides a summary of preserved specimens associated with sequences and their geographical locations.
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<td>Archidendron brevifolium (F.Muell.) I.C.Nielsen</td>
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<td>Between Stracke homestead and Stracke River, Queensland, Australia</td>
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<td>Archidendron brevifolium (F.Muell.) I.C.Nielsen</td>
<td>Z141</td>
<td>Cairns, cultivated in garden, Queensland, Australia</td>
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<td>Archidendron jiringa (Jack) I.C.Nielsen</td>
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<td>Kao Chong Botanical Garden, Thailand</td>
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<td>Mirlia, Ulu Belait, Brunei</td>
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<td>Lake Road near Cairns, Queensland, Australia</td>
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 Preserved specimen | Associated sequences | Taxon name/ MOTU | Sample ID | Location | Specimen code (InstCode and/or CollCode + Catalogue #) | Geolocation name / locality | GPS Coordinates
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JA63  
Lake Road near Cairns, Queensland, Australia  
145.6693°E, 16.875165°S

**Archidendron lucyi** F. Muell.  
JA68  
Cape Tribulation Road, adjacent to Coconut Beach resort, Queensland, Australia  
145.45726°E, 16.11345°S

**Archidendron lucyi** F. Muell.  
JA69  
Cairns, cultivated in garden, Queensland, Australia  
145°46'15"E, 16°55'13"S

**Archidendron megaphyllum** Merr. & L.M. Perry  
JA03  
Central Province; Mt Gerebu, trail towards summit ridge, PNG  
147.646°E, 9.46595°S

**Archidendron microcarpum** (Benth.) I.C. Nielsen  
JA06  
Near Sumpa, Sarawak, 112°10'E, 1°20'N

**Archidendron muellerianum** (Maiden & R.T. Baker) I.C. Nielsen  
JA112  
Big Scrub Flora Reserve, NNE of Lismore, New South Wales, Australia  
153°19'44.880"E, 28°38'18.228"S

**Archidendron parviflorum** Pulle  
JA01  
Morobe Province; Siboma, Sayama, above Sayama Creek, to E Camp 1, PNG  
147.302°E, 7.52557°S

**Archidendron pellitum** (Gagnep.) I.C. Nielsen  
JA34  
108°27'E, 11°57'N

**Archidendron ptenopum** Verdc.  
JA116  
Wanang village, Madang, PNG  
145°10.631'E, 5°14.238'S

**Archidendron quocense** (Pierre) I.C. Nielsen  
JA13  
Ko Rang Yai, Thailand  
102°23'E, 11°48'N

**Archidendron ramiflorum** (F. Muell) Kosterm.  
Z111  
Atherton Arboretum. Tag #1652, Queensland, Australia  
145°29'8.6"E, 17°15'31.4"S

**Archidendron sp. nov. in obs.**  
JA85  
Pulan Baun, Aru Island Indonesia  
134°35'E, 6°30'S

**Archidendron syringifolium** (Kosterm.) I.C. Nielsen  
JA41  
Agu River branch of the middle Fly River, PNG  
141.166667°E, 6.966667°S

**Archidendron ramiflorum** (F. Muell) Kosterm.  
JA67  
Regeneration plot, Daintree Rainforest Observatory, Queensland, Australia  
153°21'57"E, 28°10'37"S

**Archidendron vaillantii** (F. Muell) F. Muell.  
JA51  
Cape Tribulation, Queensland, Australia  
145°27'E, 16°6'15"S

**Archidendron vaillantii** (F. Muell) F. Muell.  
JA52  
Along Paluma Dam Road, Ethel Creek, Queensland, Australia  
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the Australian Genome Research Facility, Melbourne. Sequences were aligned in Geneious v.8.1.4 (Biomatters Ltd.) and assessed for variability between the samples. The most variable loci were then used in a targeted amplicon sequencing (TAS) approach (McLay et al. 2021), sequencing pooled amplicons on an Illumina MiSeq. For this, additional internal primers were designed for the five loci that had a total amplicon length greater than 500 bp, in order to produce shorter amplicons that could be fully sequenced using a 500-cycle sequencing kit. These primers were designed using Primer 3 v.2.3.4 (Rozen and Skaletsky 2000) implemented in Geneious v.8.1.4 (Biomatters Ltd.), selecting priming sites in conserved regions across the nine sequenced individuals.

Library preparation followed the two-step PCR process outlined in McLay et al. (2021). The first step used the region-specific primers to amplify each locus individually for each sample. Initial PCR reactions included 1x MyTaq Buffer (Bioline), 1.2 μl of MgCl₂ 2.5 M (Bioline, 100 mg mL), 1.2 μl of dimethyl sulfoxide (DMSO, 99.5%; Sigma-Aldrich), 3 μl of each “tailed” primer (10 μM), 0.375 U of MyTaq (Bioline), 100 ng of gDNA, and ultra-pure water to make up for 16 μl volume. Variations in these reactions are noted in Suppl. material 1 for specific loci. Conditions for PCR were based on those of Choi et al. (2006), Shaw et al. (2007), and Ariati et al. (2006) with modifications as required to obtain successful amplifications (Suppl. material 1). To estimate amplicon concentration to decide the volume of PCR product for amplicon pooling, 2.2 μl of PCR product and 2.5 μl of molecular ladder (EasyLadder I, Bioline) were run on 1.5% agarose. A total of 120 ng of each nuclear DNA (ncDNA) region PCR product and 20 ng of each chloroplast region PCR product were pooled in the same well of a 96-well plate. The ncDNA were pooled in a higher concentration to account for the possible presence of different alleles. Pooled samples were cleaned with 1.5 × Serapure beads (Rohland and Reich 2012).

The second step used qPCR to add unique Illumina indexing barcodes to each sample for the pooled amplicons. Indexing PCR reactions consisted of 5 μM of each of index primer (McLay et al. 2021), 3 μl of pooled amplicons, 1 × Kapa HiFi ReadyMix (Biosystems) and ultra-pure water to make up a total of 25 μl reaction. Conditions for PCR were 95 °C for 1 min, followed by 13 cycles of 98 °C for 50 sec, 67 °C for 50 sec, and 72 °C for 20 sec, and a final extension at 72 °C for 30 sec. Each sample was then cleaned with 1.4 × Serapure beads and concentrations were quantified using fluorescence in an EnSpire multimode plate reader. In total, 10 ng of each indexed and cleaned sample was pooled together. The final pooled library was cleaned with 1.5 × Serapure bead-to-sample ratio and the library was submitted to the Australian Genome Research Facility, Melbourne for sequencing on an Illumina MiSeq using a 500 cycle MiSeq v2 Nano Kit.

Data analysis

Sequences obtained by Sanger sequencing were aligned by individual locus in Geneious v.8.1.4 (Biomatters Ltd.) and a consensus sequence was generated and used as the reference for the reads obtained by TAS. The demultiplexed TAS Illumina MiSeq files were imported into Geneious v.8.1.4. Reads were trimmed to remove adapters and low-
quality sequence. The map-to-reference option was selected to map reads for each sample to the different reference loci using High Sensitivity/Medium settings and a minimum mapping quality of 20. A consensus sequence for each locus was generated for each individual with Generate Consensus Sequence (Threshold = 65%, with Ns called if coverage was less than 10). The forward and reverse reads of the low-copy nuclear genes (LCNG) overlapped so it was possible to phase these loci into separate alleles, but this was not possible for the nuclear ribosomal DNA loci (ETS and ITS) as the reads were not overlapping due to unexpected length variation in both of these loci. Alignments of individual consensus sequences for each locus were generated using MUSCLE (Edgar 2004) in Geneious v.8.1.4 and adjusted manually. For each LCNG, samples with multiple alleles were assessed for topological concordance between the different copies using neighbour-joining trees (using the Geneious tree-builder, HKY model) and NeighbourNet networks (SplitsTree4, default settings, Huson and Bryant 2006), to ensure that a conflicting signal was not introduced from distantly related allelic variants (see Suppl. material 2: SHMT network and tree and Suppl. material 3: RBPCO network and tree). Allelic variants within samples were largely concordant with one-another permitting consensus sequences for those samples to be used for subsequent phylogenetic analyses.

Alignments of all nuclear loci (ncDNA; with consensus sequences for LCNG alignments) were analysed individually to explore gene tree topologies in IQ-TREE v.1.6.12 on the web server (http://iqtree.cibiv.univie.ac.at/, Trifinopoulos et al. 2016) with support estimated with 1,000 ultra-fast bootstrap replicates (UFBS) (Minh et al. 2013). After comparing topologies, four ncDNA loci (ETS, ITS, RBPCO, SHMT) were concatenated into a single matrix as no major incongruencies were observed. The combined ncDNA dataset was partitioned into six partitions corresponding to each locus with the ITS region further divided in ITS1, 5.8S and ITS2 for subsequent analyses. IQ-TREE was used to perform maximum likelihood (ML) analyses on the concatenated ncDNA alignment. The analysis was run with the alignment partitioned and allowing ModelFinder (Kalyaanamoorthy et al. 2017) to identify the optimal substitution models for each partition (Table 2). Node support was estimated using 1,000 UFBS. Bayesian Inference (BI) was performed, with the alignment partitioned by locus. The best model of substitution for each partition was estimated with IQ-TREE model selection using the options: selection criteria of Bayesian (BIC), candidate models JC, F81, K80, HKY, SYM, GTR, heterogeneity types I, G, I+G, and the genomic source of nuclear (Table 2). MrBayes v.3.2.7a (Ronquist et al. 2012) was run using the CIPRES Science Gateway (Miller et al. 2010). Two parallel runs each with eight Monte Carlo Markov Chains were run for five million generations, sampling a tree every 1,000 generations and a burn-in of 25%.

A consensus network of the combined ncDNA dataset was constructed in SplitsTree4 (Huson and Bryant 2006) using the last 101 sampled BI trees (edge weights = mean, threshold = 0.05). This method allows for the visualisation of conflict in a set of trees and provides an alternative method of interpretation to a single fixed topology of a consensus tree.

All chloroplast (cpDNA) loci were concatenated into a single matrix for phylogenetic analyses. IQ-TREE was used to perform ML analyses on the cpDNA matrix, with
the alignment partitioned by locus, using ModelFinder to identify the optimal substitution model for each locus, and support was estimated using 1,000 UFBS replicates. The resulting topology was very poorly supported (though similar groups to the ncDNA phylogeny were discovered within the genus *Archidendron*). To further investigate cpDNA relationships within *Archidendron*, the outgroups were removed, and the IQ-TREE analysis was performed on the reduced dataset. The UFBS replicates were then used to create a consensus network in SplitsTree4 (edge-weights = mean, threshold = 0.20).

**Pollen morphology of Archidendropsis subg. Basaltica**

Pollen size and surface texture are key morphological features differentiating the subgenera of *Archidendropsis* but one of the three species of subg. *Basaltica* (*A. xanthoxylon* (C.T. White & W.D. Francis) I.C. Nielsen) was not examined by Nielsen et al. (1983b). To fill this gap and ensure consistency of results with published data, pollen from *A. xanthoxylon* (BRI AQ0199126, BRI AQ0874091, BRI AQ0199129 and BRI AQ0648303) and *A. basaltica* (F. Muell.) I.C. Nielsen (BRI AQ1003764, BRI AQ0199029, BRI AQ0625292 and BRI AQ0648454) of subg. *Basaltica* was examined. Pollen grains were obtained from flowers of herbarium specimens under a Zeiss dissecting microscope at the Queensland Herbarium (BRI) using clean forceps and a fine brush. Samples were mounted on aluminium stubs using double-sided carbon tabs and coated with gold using an Agar Scientific Automatic Sputter Coater. Pollen grains were observed and photographed using a Phenom G2 5keV (kiloelectron-volt) desktop scanning electron microscope (PhenomWorld). Pollen diameter for 10 grains of *A. basaltica* and eight grains of *A. xanthoxylon* was measured using ToupView (TOUPTEK PHOTONICS) software; overall fewer grains were available on specimens of *A. xanthoxylon* for microscopy.

**Results**

**Targeted amplicon sequencing loci**

Of the eight nuclear loci only four were included in the final phylogenetic analyses: SHMT, RBPCO, ITS and ETS. ETS and ITS amplified well, were variable, and are
commonly used phylogenetic markers in Caesalpinioideae phylogenetic studies. Of the LCNGs, SHMT was the most informative, followed by RBPCO; allelic variation was found in some individuals for all LCNGs. Exploring allelic variation in the SHMT (36 samples with alleles) and RBPCO (24 samples with alleles) showed that for samples with more than one allele, the copies were closely related to each other (Suppl. material 2: SHMT network and tree and Suppl. material 3: RBPCO network and tree). Two LCNGs were excluded because few individuals of the target genera were successfully sequenced; only 12 sequences of Archidendron and two sequences of Archidendropsis were obtained for AlGP, and only 16 sequences of Archidendron and one Archidendropsis were obtained for Eif3E. The remaining two LCNG loci (CYB6 and UDPG) are not included in the analyses due to their short lengths, 240 bp and 202 bp respectively, and lack of variation.

Of the four chloroplast loci, trnK-matK was the most informative, followed by psbD-trnT and then trnV-ndhC. However, only one of the three blocks of trnV-ndhC was successfully sequenced. The internal primers designed allowed 100% coverage for the trnK-matK, 81% coverage for the psbD-trnT, and less than 30% coverage for the trnV-ndhC. It was not possible to obtain sequences for all samples for all blocks in which the three cpDNA regions were divided; as a result the cpDNA dataset was patchy. The trnL-rplB2 intergenic spacer did not amplify well, with 10 samples partially sequenced, and it was not included in final analyses.

Phylogenetic analyses

The topologies of the combined ncDNA Bayesian and IQ-TREE analyses were congruent (nodes supported with UFBS ≥ 95; PP ≥ 0.90) and the Bayesian tree is presented (Fig. 2A,B). The Archidendron clade was recovered as monophyletic (PP 1.0) with six well supported clades (A–F) resolved within it. However, the relationships between clades A–F were not well resolved or supported with a polytomy in the backbone of the phylogeny. Clade A (PP 0.99) includes all three species of Archidendropsis subg. Basaltica, clade B (PP 1.0) includes the three samples of Pararchidendron pruinosum (Benth.) I.C. Nielsen, and clade C (PP 1.0) includes the two sampled representatives of Archidendropsis subg. Archidendropsis. Four monophyletic genera are grouped together in clade D (PP 1.0), with Acacia sister to Paraserianthes in clade D1 (PP 1.0) and Falcataria sister to Serianthes (PP 1.0) in clade D2 (Fig. 2A). Clade E (PP 1.0) comprises all but two sampled representatives of Archidendron ser. Clypeariae, and all other samples of Archidendron are placed in clade F (PP 1.0). Clades C, D and Wal laceodendron are related (PP 0.98) and together are sister to Clade E (PP 0.96; Fig. 2A).

Within Archidendron, only one of Nielsen’s eight series is resolved as monophyletic (ser. Ptenopae) within subclade F1 (Fig. 2A). Clade E, the Clypeariae clade had two main lineages and several smaller supported subclades within them. Clade F, the Archidendron s.s. clade is segregated into three well supported subclades: the lucyi subclade (F1, PP 1.0) that includes three fully supported lineages; the grandiflorum subclade (F2, PP 1.0) that is poorly resolved; and the vaillantii subclade (F3, PP 1.0) that comprises two well supported lineages (PP 0.99; Fig. 2A–C).
Figure 2. Combined ncDNA phylogeny of the Archidendron clade. The Bayesian Inference (BI) cladogram, phylogram, and consensus network for the combined ncDNA dataset are presented. The star indicates the Archidendron clade sensu Koenen et al. (2020). Nodes with PP = 1.0 are shown in bold while other nodes with PP ≥ 0.50 are noted under the node. Clades are labelled with letters above the node. Coloured bars to the right of clades are names discussed in the text. Nielsen's series of Archidendron are shown as coloured circles next to the sample name; key to colour and series in legend. Clades are labelled as per the clades of Archidendron s.s. clade. 

Outgroup

Archidendropsis subg. Basaltica

Archidendron

Archidendropsis subg. Archidendropsis

Acacia

Falcataria

Serianthes
Of the 12 species of *Archidendron* that included more than one accession, seven are monophyletic (*A. glabrum* (K. Schum.) K. Schum. & Lauterb., *A. kanisii* R.S. Cowan, *A. lucyi* F. Muell., *A. muellerianum*, *A. ramiflorum* (F. Muell.) Kosterm., *A. vaillantii* (F. Muell.) F. Muell. and *A. whitei*), one is unresolved (*A. lovelliae* (F.M. Bailey) I.C. Nielsen), and four are not monophyletic (*A. clypearia* (Jack) I.C. Nielsen, *A. grandiflorum* (Sol. ex. Benth.) I.C. Nielsen, *A. hendersonii* (F. Muell.) I.C. Nielsen and *A. hirsutum* I.C. Nielsen). Three of the four samples of *A. clypearia* form a clade (within clade E, Fig. 2; PP 1.0) with *A. borneense* (Benth.) I.C. Nielsen nested among them. One sample of *A. hendersonii* (JA45) is related to *A. grandiflorum* within clade F2; all other samples of *A. hendersonii* (Z114, JA103, JA44) form a clade within F3 (PP 1.0; Fig. 2A). Another species falling in both subclades F2 and F3 is *A. hirsutum*, with one sample (JA46) related to *A. forbesii* Baker f. and *A. lovelliae* in subclade F2 (PP 0.99), and the other two (Z113 and JA86) forming a sister pair in subclade F3 (PP 1.0; Fig. 2A).

The consensus network of the final 101-sampled BI trees shows the degree of topological uncertainty between the genera in the Archidendron clade (Fig. 2C). While each respective genus is well-supported as monophyletic (except *Archidendropsis* and *Archidendron* as described above) the relationships between the genera are highly uncertain, reflecting the lack of support in the consensus phylogenies. However, the network reinforces the distinction between the two clades of *Archidendropsis*, and the distinction of the Clyperiae clade from the rest of *Archidendron*.

The phylogeny of the three cpDNA loci combined lacks support for nearly all nodes (Suppl. material 4: cpDNA tree). Of the supported nodes there are two that are incongruent with the ncDNA tree (Fig. 2): *Paraserianthes* is sister to *Falcataria* (UFBS 100), and *A. harmsii* Malm is supported in the grandiflorum subclade (UFBS 95) sister to *A. grandiflorum* JA100 (UFBS 97; Suppl. material 4: cpDNA tree). The consensus network of the UFBS replicates (with splits present in at least 20% of trees) reflects the patterns in the ncDNA phylogeny, with four distinct groupings within *Archidendron* (Fig. 3). Within these groupings, several individuals are placed in different clades to the ncDNA tree: *A. hendersonii* JA45 is placed in the vaillantii subclade rather than the grandiflorum subclade, and *A. harmsii* JA74 is in the grandiflorum subclade rather than the lucyi subclade (Fig. 3).

**Pollen morphology of Archidendropsis subg. Basaltica**

The pollen measurement results are consistent with Nielsen et al. (1983a, 1983b). The pollen of the two species examined (*A. basaltica* and *A. xanthoxylon*) are aggregated into symmetrical 16-celled polyads with a diameter of 55–62 μm for *A. basaltica* and 62–68 μm for *A. xanthoxylon* (Fig. 4). Fossules were present on the surface of all grains of both species, but they were fainter on the peripheral cells compared to the central ones and overall fainter on *A. basaltica* compared to *A. xanthoxylon* (Fig. 4).
Phylogeny of Australasian mimosoid legumes *Archidendron* and *Archidendropsis*

**Discussion**

**Phylogeny of the Archidendron clade**

Our study presents the most taxon-rich sampling of the Archidendron clade of any phylogenetic analyses to date. We confirm that the Archidendron clade sensu Koenen et al. (2020) of Indomalayan-Australasian genera (*Acacia, Archidendron, Archidendropsis, Falcataria, Serianthes, Pararchidendron, Parasianthehes* and *Wallaceodendron*) is robustly supported, yet the relationships between the constituent clades are poorly resolved and lack support. This result is not unexpected given we used only four ncDNA loci and that phylogenomic studies based on hundreds of loci also yield short branches with low support across the backbone of the Archidendron clade (Koenen et al. 2020; Demeulenaere et al. 2022; Ringelberg et al. 2022). It has been suggested that this lack of resolution may be the result of extremely rapid speciation and that the backbone of this clade could be best regarded as a polytomy within the Ingoid legumes (Koenen et al. 2020). The differences in published topologies of the Archidendron clade are illustrated in Demeulenaere et al. (2022) but it is clear that further work based on increased sampling of phylogenomic data is required to uncover the evolutionary history of the clade.
Despite the poorly resolved backbone of the Archidendron clade, many clades within it are robustly supported and corroborate published phylogenies, as well as shedding new light on the genera *Archidendron* and *Archidendropsis* (Fig. 2). Four genera of the Archidendron clade are confirmed to be monophyletic — *Acacia* (Miller and Bayer 2001; Luckow et al. 2003; Miller et al. 2003; Brown et al. 2008), *Falcataria* (Brown et al. 2011), *Pararchidendron* and *Serianthes* (Demeulenaere et al. 2022) — and the previously suggested non-monophyly of *Archidendron* and *Archidendropsis* (Brown et al. 2008, 2011; Iganci et al. 2016; Demeulenaere et al. 2022; Ringelberg et al. 2022) is confirmed and clarified by increased sampling within these genera.

Figure 4. Scanning electron micrographs of *Archidendropsis* subg. *Basaltica* pollen. *Archidendropsis xanthoxylon* (A BRI AQ0199126 and B BRI AQ0874091) and *Archidendropsis basaltica* (C BRI AQ0199029 and D BRI AQ01003764).
Phylogeny of Australasian mimosoid legumes Archidendron and Archidendropsis

Phylogenetic relationships within Archidendron

The genus Archidendron is not monophyletic, and the eight series, while useful for identification purposes, do not coincide with evolutionary lineages (Fig. 2). The only series confirmed to be monophyletic was series Ptenopae from the island of New Guinea, the smallest series comprising just two species with two-winged leaf rachises and pinnae: A. ptenopum Verdc. and A. hispidum (Mohlenbr.) Verdc. (Nielsen et al. 1984b). The monophyly of series Calycinae and Pendulosae was not tested, as only one species of each was sampled, however, all other series (Archidendron, Bellae, Clypeariae, Morolobiae, and Stipulatae) are not monophyletic. Archidendron is instead resolved into two well supported lineages, one of which is primarily distributed in western Malesia and mainland Asia (the Clypeariae clade; clade E, Figs 1–3) and the other (the Archidendron s.s. clade; clade F, Figs 1–3) mostly restricted to eastern Malesia and Australia. These two lineages have been identified in previous phylogenetic studies but the sampling for each was extremely limited, with at most seven species of one lineage included (Brown et al. 2008, 2011; Iganci et al. 2016; Demeulenaere et al. 2022; Ringelberg et al. 2022). The further segregation of the Archidendron s.s. clade into three well supported lineages, the lucyi (F1), the grandiflorum (F2), and the vaillantii subclades (F3; Figs 2–3), is novel.

These three subclades of the Archidendron s.s. clade reflect geographic distributions to some extent, but no macromorphological characters have been identified to clearly delineate them. The grandiflorum and vaillantii subclades are predominantly Australian with some southern New Guinean species included, while the lucyi subclade is geographically more broadly distributed in the Lesser Sunda Islands, the Moluccas, through New Guinea to the Solomon Islands with only one species, A. lucyi, extending into northern Australia. Morphologically, the lucyi subclade includes all the sampled species lacking stipules that are not from ser. Clypeariae (i.e. A. calliandrum de Wit, A. harmsii, and A. glabrum), although stipules are reported for other species in this clade, three with stipular glands (A. lucyi, A. megaphyllum Merr. & L.M. Perry, Archidendron sp. nov. JA85), two with stipules only (A. ptenopum and A. hispidum) and A. parviflorum Pulle having both stipular glands and stipules (AAU Balgooy 6769; Nielsen et al. 1984b). All sampled species in the grandiflorum and vaillantii subclades have stipules, except A. arborescens (Koster.) I.C. Nielsen and A. forbesii, which have stipular glands (BM000946689; BRI AQ0380081; BRI AQ052589; Nielsen et al. 1984b) The placement of an undescribed species (Archidendron sp. nov. JA85) from the Aru Islands (Moluccas) in the lucyi subclade fits the geographic range. Ivan Nielsen noted this as a putative new species in October 1998 (AAU Balgooy 6769) but it does not align with any of the 20 imperfectly known species he outlined (Nielsen et al. 1984b), highlighting that further taxonomic work is required.

Three species in the Archidendron s.s. clade were not resolved as monophyletic (Fig. 2A), although it is unlikely these are issues with species delimitation. The paraphyly of A. grandiflorum (Fig. 2), a morphologically consistent species across a large geographic range (Brown pers. obs.), could be the result of potentially rapid and recent divergence.
or may be due to insufficient phylogenetically informative characters in this study. The latter could also apply to the polyphyletic species (\textit{A. hendersonii} and \textit{A. hirsutum}), as \textit{A. hendersonii} JA45, which is placed separately from the other conspecific samples is missing data for two of the four ncDNA loci (Table 1). However, this was not the case for \textit{A. hirsutum} JA46. Re-examination of the vouchers of all accessions of \textit{A. hendersonii} and \textit{A. hirsutum} confirmed their identifications, suggesting that incomplete lineage sorting or paralogy problems associated with one or more nuclear loci could explain these non-monophyletic species; further data are required to investigate this.

The Clypeariae clade (clade E, Figs 2–3) includes all sampled species of ser. \textit{Clypeariae} (19/51), except one accession of \textit{A. clypearia} (JA95) from Papua New Guinea and \textit{A. pellitum} (Gagnep.) I.C. Nielsen from Vietnam. Series \textit{Clypeariae} was previously recognised in \textit{Pithecellobium} as section \textit{Clypearia} until Nielsen et al. (1984b) expanded \textit{Archidendron} based on evidence from shared wood anatomy, inflorescence and pod morphology (Nielsen et al. 1984b). Characters of the pods are also useful to differentiate series \textit{Clypeariae} from the rest of \textit{Archidendron}. Nielsen et al. (1984b) described six pod types and most species of ser. \textit{Clypeariae} have pod type 2 (long funicle, opens ventral suture first) or 6 (straight pods with overgrown seeds), while the other species primarily have pod type 1 (opens dorsal suture first, short funicles). Seeds of ser. \textit{Clypeariae} are usually flattened and are not embedded in the pericarp, which is possibly linked to characteristics of the pod, such as dryness (de Wit 1942; Nielsen 1981, 1992; Nielsen et al. 1984b). Additionally, the combination of lack of stipules and solitary, stipitate ovaries delineates ser. \textit{Clypeariae} (Nielsen et al. 1984b). Individually though, these characters are not diagnostic, as some species with sessile ovaries are placed in ser. \textit{Clypeariae} (e.g. \textit{A. occultatum} (Gagnep.) I.C. Nielsen and \textit{A. turgidum} (Merr.) I.C. Nielsen), other species lacking stipules are placed in series \textit{Archidendron} (e.g. \textit{A. harmsii} and \textit{A. tjendana} (Kosterm.) I.C. Nielsen), and two Philippine species of ser. \textit{Clypeariae} (\textit{A. apoense} (Elmer) I.C. Nielsen and \textit{A. merrillii} (J.F. Macbr.) I.C. Nielsen) have more than one ovary but both are stipitate (Nielsen et al. 1984b). Given these morphological differences of ser. \textit{Clypeariae} from the rest of \textit{Archidendron}, together with the non-monophyly of the genus, there are grounds for segregating \textit{Clypeariae} as a distinct genus; however, we are not proposing such a taxonomic change here for several reasons. First, there are many shared morphological characters between species of \textit{Archidendron} s.l.; second, the shallow backbone of the ncDNA tree remains poorly supported with topological uncertainty between lineages; third, the placement of two species of ser. \textit{Clypeariae} within the \textit{Archidendron} s.s. clade (clade F; \textit{A. clypearia} var. \textit{velutinum} (Merr. & L.M. Perry) I.C. Nielsen and \textit{A. pellitum}) raises further doubts; and fourth, phylogenetic sampling of species remains incomplete. All these issues suggest that denser taxon sampling and larger phylogenomic datasets are required before re-classifying \textit{Archidendron} as two genera.

\textit{Archidendron clypearia} is the most widespread species of \textit{Archidendron}, found from India through to Papua New Guinea. The morphological variation within \textit{A. clypearia} has been used to recognise four infraspecific taxa (Legume Phylogeny Working Group 2021): subsp. \textit{clypearia}, subsp. \textit{subcoriaceum} (Thwaites) M.G. Gangop & Chakrab.,
var. sessiliflorum (Merr.) I.C. Nielsen, and var. velutinum. The one accession of A. clypearia placed outside the Clypeariae clade (JA95) (Fig. 2A) has been identified as var. velutinum (Brown, pers. obs. of CANB525617; previously only identified to species level by the collector), the only infraspecific taxon found in eastern Malesia (Sulawesi, Moluccas and PNG). The three other samples of A. clypearia included in the phylogeny have not been assigned to infraspecific taxa but they are not likely var. velutinum, as they are from Malaysia and Vietnam and lack the woolly to velutinous hairs on the lower surface of the leaflets (Brown per. obs.). Taxonomic revision and denser phylogenetic sampling of A. clypearia from across its morphological and geographic range is required to verify this placement, delineate the taxa and investigate if var. velutinum should be raised to species level (Merrill and Perry 1942) or if there are intermediate forms as suggested by Kostermans (1966). The only other species of series Clypeariae that extends into eastern Malesia, A. palauense (Kaneh.) I.C. Nielsen, from the Moluccas through to the Solomon Islands (Nielsen et al. 1984b), was not sampled here. There are no obvious morphological characters that support placement of A. pellitum outside the Clypeariae clade, as it has the full combination of diagnostic characters of ser. Clypeariae: compressed pods with a long (3–5 mm) funicle, stipitate single ovary and no visible stipules (US 2515891; P01818442; Nielsen 1981). In addition, no evidence of paralogy in the nuclear loci of A. pellitum and A. clypearia var. velutinum (JA95) was noted in this study; all sequences suggest they fall in the A. lucyi subclade.

The last revision of the genus Archidendron (Nielsen et al. 1984b) significantly advanced our understanding of the genus but more detailed taxonomic study is still required, focusing especially on the large number of species known from incomplete material and widespread morphologically variable species, such as A. clypearia. To resolve the backbone of the Archidendron clade and inform decisions about generic delimitation to deal with the non-monophyly of Archidendron, we recommend further sampling of ser. Clypearia, particularly from the Wallacean region of Malesia (i.e. Moluccas, Sulawesi, Philippines), together with further genomic sampling.

**Phylogenetic relationships within Archidendropsis**

While Archidendropsis is not monophyletic, its two subgenera (Archidendropsis and Basaltica) are (Fig. 2). The species within each subgenus have long been recognised as closely related (Bentham 1875; Nielsen 1981) but the two subgenera themselves have not always been associated with each other. For example, Bentham (1875) placed the species of each subgenus in different sections of Albizia based on inflorescence shape. Species of subgenus Archidendropsis that have flowers arranged in cylindrical spikes were placed by Bentham (1875) in Albizia section Lophantha Benth. (an illegitimate name later corrected to Albizia section Pachysperma (Benth.) Fosberg by Fosberg (1965)). Within this section they were separated from the other taxa, which are now recognised as Paraserianthes, into series Platypermae Benth. because they have flattened, broadly orbiculate seeds (Bentham 1875). The two species of subgenus Basaltica known at that time (A. basaltica and A. thozetiana (F. Muell.) I.C. Nielsen) were placed by Bentham in his
large section *Eualbizzia* distinguished by flowers in globular heads and flattened orbicular seeds (Bentham 1875). Within that section, these taxa were placed into series *Obtusifolia*, which corresponds to the Australian species with 1–2 jugate leaves, ovate, oblong or obtuse leaflets, short petioles, pedunculate heads in the axils, and small sessile flowers.

It was only recently that the species of the two subgenera were united within *Archidendropsis* by Nielsen (1983) based on characters of the fruit and seed: pods dehiscent along both sutures, and seeds that are winged, thin-walled and lack a pleurogram. However, Nielsen himself questioned whether the subgenera should be congeneric, noting that if they were not, “the evolution of the winged thin walled seeds without pleurogram should have happened twice” (Nielsen et al. 1983a: p. 337). The results presented here (Fig. 2) alongside two recent phylogenomic analyses (Demeulenaere et al. 2022; Ringelberg et al. 2022) show that the two subgenera of *Archidendropsis* do not form a monophyletic group, suggesting these seed characteristics are indeed the result of convergent evolution.

The presence of a pleurogram is common in mimosoid genera (Gunn 1984), and is considered to have evolved multiple times (Maumont 1993). Within the Archidendron clade, *Archidendron* and *Archidendropsis* are the only two genera whose seeds lack a pleurogram (Nielsen 1992). The absence of a pleurogram has been associated with short-lived ‘recalcitrant’ seeds (i.e. seeds which lack dormancy and can be viviparous; Nielsen 1992) and has been thought to be an adaptive response to humid environments (Corner 1951 in Nielsen 1992; Maumont 1993). Like the absence of a pleurogram, winged seeds are also rare in mimosoids occurring in only eight genera, including *Archidendropsis* (Gunn 1984). The possession of a winged seed has been suggested to be an adaptation for wind-dispersal but there have been no published observations of this in *Archidendropsis* (Gunn 1984; Nielsen 1992). The short viability of *Archidendropsis* seeds has been linked to the restricted geographic ranges of individual species (Nielsen 1983). However, humidity may be a more important determinant of these distributions, as the ranges of the two Australian species occurring in drier, non-rainforest habitats are more than 10 times larger than the rainforest species (e.g. *A. basaltica* ≥ 750,000 km² compared to *A. xanthoxylon* c. 8,750 km² (AVH 2021)). The habitats of *A. basaltica* and *A. thozetiana* are also more open than for *A. xanthoxylon*, but these two species generally have narrower wings on their seeds than the rainforest species *A. xanthoxylon* (Cowan 1998), suggesting that the wing is unlikely to have an impact on wind dispersal. Morphological features that have been used to unite the two subgenera in *Archidendropsis* are thus homoplasicous and not useful for generic delimitation.

The non-monophyly and clear morphological distinctions between them means that the two subgenera can no longer be treated as congeneric and need to be placed in separate genera. As the type of *Archidendropsis* (*A. fulgens* (Labill.) I.C. Nielsen) is from subg. *Archidendropsis*, it is subg. *Basaltica* that requires a new name. No name exists at the generic level for these taxa, as they have previously been placed in *Acacia*, *Albizia* and *Archidendropsis* (Mueller 1859; Bentham 1875; Fosberg 1965; Nielsen 1983), names which are all typified by other taxa.

In addition to the aforementioned morphological differences between the two subgenera, species of subg. *Basaltica* are endemic to Australia, whereas those of subg. *Archidendropsis* are found in New Caledonia, New Britain, the Solomon Islands and
Phylogeny of Australasian mimosoid legumes Archidendron and Archidendropsis

on the island of New Guinea (Fig. 1B). Furthermore, there are several pollen characters separating the two subgenera (Nielsen et al. 1983a). Pollen of subg. Basaltica has isometric channels in the tectum and is aggregated into smaller polyads (55–68 μm), cf (80–120 μm) for subg. Archidendropsis where the tectum has non-isometric channels (Fig. 4; Nielsen et al. 1983a). The pollen surface of subg. Basaltica has fossules on the central cells, with either faint fossules or smooth peripheral cells, while in subg. Archidendropsis the surface of all pollen cells has small rounded areoles or deep fossules (Fig. 4; Nielsen et al. 1983a). Species of subg. Basaltica have sessile flowers arranged in globose pedunculate heads, rather than in spikes or racemes. Although one species of subg. Archidendropsis, A. fournieri (Vieill.) I.C. Nielsen, also has flowers arranged in globose pedunculate heads, it does not share the other diagnostic characters of subg. Basaltica, it is endemic to New Caledonia, its seeds are not winged, and the diameter of the pollen polyads is larger, fitting within the size range for subg. Archidendropsis (Nielsen 1983). Another character noted by Nielsen et al. (1983a) to differentiate the two subgenera, was the shape of the stipules, with those of subg. Basaltica being small and often developed into stipular spines (to 1.2 mm long; Brown pers. obs.; Fig. 5F) that are early caducous. However, the stipules of A. xanthoxylon were not recorded by Nielsen et al. (1983a) and are not like other Australian species being 1.2–3 mm long, ovate to triangular, dark gland-like and persistent (Brown, pers. obs., BRI AQ022813, BRI AQ0234095, BRI AQ0771148, BRI AQ199127, BRI AQ0199128; Fig. 5G). These stipules do differ, however, from those of the species of subg. Archidendropsis which, if present, are usually small (c. 1 mm), ovate or filiform and often caducous (Nielsen 1983).

Flowers arranged in globose heads, seeds lacking a pleurogram with a narrow peripheral membranous wing and flat, narrowly oblong, brown pods opening along both sutures distinguish this new genus from other Australian mimosoid legumes, and the keys in Flora of Australia (Cowan 1998) and available on KeyBase (Bean 2021; KeyBase 2021) still remain suitable.

**Taxonomic treatment**

*Heliodendron* Gill.K. Br. & Bayly, gen. nov.
urn:lsid:ipni.org:names:77303797-1
Fig. 5

**Diagnosis.** A genus of mimosoid legumes similar to *Archidendropsis* but differing in the following combination of features: inflorescences of glomerules, calyx and corolla with hairs (restricted to the lobes in *H. xanthoxylon*); stipules either small (to 1.2 mm) rigid and caducous or glandular (1.2–3 mm long) and persistent; pollen arranged in polyads diameter of 55–68 μm; pollen tectum with isometric channels. In contrast, *Archidendropsis* has inflorescences of spikes, spiciform racemes, racemes or in one species glomerules, but when in glomerules the calyx and corolla are glabrous; stipules (if present) either small (c. 1 mm) ovate or filiform and often caducous, or large auriculate, orbicular, or cordate and persistent; pollen polyad diameter of 80–120 μm, pollen tectum with non-isometric channels.
Figure 5. Morphology of Heliodendron. Plate showing diagnostic features of the new genus Heliodendron
A inflorescence of H. thozetianum, Hazelwood Gorge, west of Mackay, Queensland (photo, Stuart Worboys, Australian Tropical Herbarium) B single flower of H. basalticum (BRI AQ0648454) showing hairs on calyx and corolla C mature bud of H. xanthoxylon (BRI AQ0874091) showing hairs on the lobes of the calyx and corolla D seeds of H. basalticum (BRI AQ0746724) E overall pod shape of H. xanthoxylon (BRI AQ0234095) F small rigid stipules of H. basalticum (BRI AQ0673898) G glandular stipule of H. xanthoxylon (BRI AQ0771148). Whole leaf showing overall leaflet size and shape of H. basalticum (BRI AQ0648454) I H. thozetianum (BRI AQ0611464), and J H. xanthoxylon (BRI AQ0874091). Habit of H. basalticum from K Bladensberg National Park, Queensland (photo, Dale Richter, Queensland Herbarium) L 65 km west south-west of Blackall, Queensland (photo, Murray Fagg, Australian Plant Image Index, Australian National Botanic Gardens).
Description. Trees or shrubs, with terete branchlets. Stipules either resembling small thorns to 1.2 mm long that are early caducous, or persistent circular-ovate glands 1–3 mm in diameter. Leaves bipinnate, pinnae 1–2 pairs with 1.5–11 leaflet pairs per pinna; glands at the junction of pinnae circular or triangular to rhombic, +/- circular glands at the junction of leaflet petiololes. Leaflets opposite, subsessile (0.2–0.7 mm) or long (3.5–7 mm) petioloate; elliptic to elliptic-lanceolate or oblong, 2–38 mm × 1.5–15 mm, glabrous to puberulous. Inflorescence of globular heads 0.5–1.7 mm in diameter, either simple or arranged into a panicle up to 35 cm long. Flowers: homomorphic, yellow to cream, sessile. Calyx 1.5–3 mm long, tubular to subcampanulate; corolla 2.5–7 mm long, tubular to narrowly campanulate. Ovary 0.8–2 mm long, solitary and shortly stipitate; stamens numerous 5–9 mm long, united basally into a tube that equals or slightly exceeds the corolla tube. Pollen 16-celled polyads with a diameter of 55–68 μm, tectum with isometric channels. Pod brown, valves chartaceous, 6–22 cm × 0.5–2.5 mm, oblong, flat and dehiscing along both sutures. Seeds lacking a pleurogram, flat, circular to ovate or obliquely ovate, 5–13 mm, with a narrow 0.2–1 mm peripheral, membranous wing. Fig. 5.

Type. Heliodendron basalticum (F. Muell.) Gill.K. Br. & Bayly ≡ Acacia basaltica F. Muell., Journal of the Proceedings of the Linnean Society, Botany 3: 146 (1859)

Etymology. From the Greek helios (sun) and dendron (tree) alluding to the endemic distribution of the genus in the Australian state of Queensland, widely known as the “sunshine state”, the globular, sun-like inflorescences of yellow flowers, and the tree habit (Fig. 5A, K, L) and also in reference to the genera Archidendropsis (in which the species were previous placed) and Archidendron (which they resemble).


Notes. We have chosen to create a new name for this genus rather than making a new combination based on the name Archidendropsis subg. Basaltica. This is because using the name “Basaltica” at generic rank would require a change of epithet for the most widespread species in the genus under Art. 23.4 of the International Code of Nomenclature for algae, fungi, and plants (Turland et al. 2018). To minimise taxonomic change, and to avoid potential confusion, we would rather that the species retains its well-known epithet, which has been in continuous use since 1859.

The genus includes the following three species, all endemic to Queensland, Australia (Fig. 1B).

Heliodendron basalticum (F. Muell.) Gill.K. Br. & Bayly, comb. nov.
urn:lsid:ipni.org:names:77303798-1

Type. Peak Downs, F. Mueller 42 (holotype: MEL 594732A image!; isotype K000822321 image!).

*Heliodendron thozetianum* (F. Muell.) Gill.K. Br. & Bayly, comb. nov.  
urn:lsid:ipni.org:names:77303799-1


urn:lsid:ipni.org:names:77303800-1


Notes. The protologue of *Albizia xanthoxylon* (White and Francis 1929) gave a location, collector name and month of the collection but did not indicate the herbarium in which the type was held, thus meaning that all specimens of this gathering could be considered syntypes. However, it appears that Nielsen inadvertently typified this taxon, according to Art. 7.11 of the ICN (Turland et al. 2018), when providing the description for the new combination of *Archidendropsis xanthoxylon* with the text “Type: Overseer Brothers, Australia, N. Queensland, Atherton District, Oct 1927, fl. fr. (holo-BRI; iso-K)” (Nielsen et al. 1983a: p. 341). We believe this satisfies the requirements of Art. 7.11 to effectively lectotypify the name, which means that the BRI specimen is the lectotype and the K specimen is the isolectotype. Interestingly, the material illustrated in the protologue is clearly the isolectotype at K, as it is the only type specimen of *Heliodendron xanthoxylon* with pods, and the structure of the inflorescence and leaves is almost identical (K000822329; White and Francis 1929).

In Flora of Australia, Cowan (1998) cited BRI as holding an isotype as well as the holotype of this taxon; however, the two sheets have the same collection details,
are labelled as sheet 1 of 2 and sheet 2 of 2, and share a single accession number (BRI AQ022813). Therefore, it is herein determined that these are the one collection, and both represent the holotype (now lectotype; BRI AQ022813).

**Conclusion**

We present the most densely sampled phylogeny of the genera *Archidendron* and *Archidendropsis* to date and confirm that both genera are not monophyletic. The well supported clades within the Archidendron clade based on four nuclear markers agree with more data-rich phylogenomic data sets now being generated. A new genus, *Heliodendron*, endemic to Queensland (Australia), is described for the Australian members of the former *Archidendropsis* subg. *Basaltica*. Further sampling of species from subg. *Archidendropsis* would be beneficial, particularly to ascertain the relationships of the globular flowered *A. fournieri* and the non-New Caledonian representatives of *Archidendropsis* s.s. While *Archidendron* is also not monophyletic, no nomenclatural changes are made, because low phylgenetic support and high topological uncertainty between genera of the Archidendron clade mean that the relationships between the two clades of *Archidendron* remain uncertain. In addition, discrete macromorphological characters need to be identified to distinguish the two lineages of *Archidendron* as the basis for generic re-delimitation. A taxonomic revision of the widespread polymorphic *A. clypearia* would aid this, as our results indicate var. *velutinum* from eastern Malesia may represent a distinct species. Phylogenomic data and additional sampling of this species would be beneficial before nomenclatural changes are made.

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South A (2017) rnaturalearth: World Map Data from Natural Earth. R package version 0.1.0. https://CRAN.R-project.org/package=rnaturalearth


Supplementary material I

Primer sequences and PCR variations

Authors: Gillian K. Brown, Javier Aju, Michael J. Bayly, Daniel J. Murphy, Todd G.B. McLay

Data type: Pdf file.

Explanation note: The reference for the primer and their PCR conditions are provided, along with the variations for PCR reagents and cycling conditions for the initial PCR in the two-step PCR process. * only used for sanger sequencing so no variations to note. Standard PCR reagents prior to variation consisted of 2X QIAGEN PCR buffer (QIAGEN), 5 mM of each dNTP (Bioline), 1 μl of each primer (10 μM), 1.25 μl of dimethyl sulfoxide (DMSO, 99.5%; Sigma-Aldrich), 1 U of Taq DNA polymerase, 100 ng of template and made up to 25 μl with ultra pure water per reaction. Reagent variations, A: not varied; B: 200 ng DNA, 1.2 μl BSA instead of DMSO; C: 200 ng DNA; D: 200ng DNA, 6 μM each primer, 1.5 μl MgCl2, 0.9 μl DMSO and 0.1 μl Taq; E: 6 μM each primer. Cycle variations: Z: 94 °C for 15 mins; 30 cycles of 94 °C for 20 sec, 61 °C for 20 sec, 72 °C for 2 mins; 72 °C for 5 mins; Y: 94 °C for 15 mins; 35 cycles of 94 °C for 20 sec, 61 °C for 20 sec, 72 °C for 2 mins; 72 °C for 5 mins; X: 94 °C for 15 mins; 35 cycles of 94 °C for 20 sec, 55 °C for 30 sec, 72 °C for 2 mins; 72 °C for 7 mins; W: 94 °C for 15 mins; 40 cycles of 94 °C for 20 sec, 50 °C for 1 min, 72 °C for 3 mins; 72 °C for 7 mins; V: 80 °C for 5 mins; 40 cycles of 95 °C for 1 min, 50 °C for 1 min with 0.3 °C/sec ramp, 65 °C for 4 mins; 65 °C for 5 mins; U: 94 °C for 5 mins; 30 cycles of 94 °C for 30 sec, 53 °C for 30 sec, 72 °C for 1 min; 72 °C for 7 mins; T: 80 °C for 5 mins; 30 cycles of 95 °C for 1 min, 50 °C for wwith 0.3 °C/sec ramp, 65 °C for 4 mins; 65 °C for 5 mins.

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Link: https://doi.org/10.3897/phytokeys.205.79381.suppl1
Supplementary material 2

SHMT network and tree
Authors: Gillian K. Brown, Javier Aju, Michael J. Bayly, Daniel J. Murphy, Todd G.B. McLay
Data type: Pdf file.
Explanation note: Neighbour-joining tree and NeighbourNet network are presented with individual samples with more than one allele coloured to highlight their positions. The samples are coloured the same in both the tree and network. The clades that are congruent with Fig. 2 (B, C, D, D1, D2, F1, F2) are labelled. The sequences from species of Albizia (Z106, JA137) were removed as they occur on a very long branch relative to the rest of the samples in the network.
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Link: https://doi.org/10.3897/phytokeys.205.79381.suppl2

Supplementary material 3

RBPCO network and tree
Authors: Gillian K. Brown, Javier Aju, Michael J. Bayly, Daniel J. Murphy, Todd G.B. McLay
Data type: Pdf file.
Explanation note: Neighbour-joining tree and NeighbourNet network are presented with individual samples with more than one allele coloured to highlight their positions. The samples are coloured the same in both the tree and network. Clade B, which is congruent with Fig. 2, is labelled.
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Link: https://doi.org/10.3897/phytokeys.205.79381.suppl3
Supplementary material 4

cpDNA tree
Authors: Gillian K. Brown, Javier Aju, Michael J. Bayly, Daniel J. Murphy, Todd G.B. McLay
Data type: Pdf file.
Explanation note: IQ-Tree of combined cpDNA loci, with all UFBS values shown. The two clades that are congruent with of Fig. 2 are labelled (A and F). Arrows indicate the placement of the two supported incongruences mentioned in the results text.
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