

TRANSFER OF THE GENUS *AULANDRA* INTO *PALAEQUIUM* (SAPOTACEAE) AND ASSOCIATED NOMENCLATURAL CHANGES

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Aulandra H.J.Lam (Sapotaceae) has hitherto been treated as a genus of tropical forest trees native to Borneo. To test whether the genus is distinct from *Palaquium* Blanco, phylogenetic analysis using maximum likelihood was performed on target capture of nuclear data, including all species currently recognised as belonging in *Aulandra*. The results confirm that *Aulandra* is nested within *Palaquium* and should be synonymised with it. One new combination, *Palaquium longifolium* (H.J.Lam) A.Phang, is made, and the application of the name *P. beccarii* discussed, resulting in the description of a new species, *Palaquium aulandrum* A.Phang.

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Introduction

The tree family Sapotaceae is readily distinguished by its copious white latex, fasciculate inflorescences, and floral characters, but generic circumscription within the family has been problematic (Pennington, 1991). A total of 122 genera were recognised by Aubréville (1964), 53 by Pennington (1991) and 73 by Swenson *et al.* (2023). Currently, 74 genera are recognised by *Plants of the World Online* (POWO, 2024) and 72 by *World Flora Online* (WFO, 2024).

Aulandra H.J.Lam is a genus endemic to Borneo and has three published species: *Aulandra beccarii* (Pierre ex Dubard) P.Royen, *Aulandra cauliflora* H.J.Lam, and the type of the genus, *Aulandra longifolia* H.J.Lam (POWO, 2024; WFO, 2024). In this paper, we note that the name *Aulandra beccarii* has been misapplied and propose a solution (see the notes under new species in the *Taxonomic treatment* section below). Chai & Yii (2002), in their account of Sapotaceae for the *Tree Flora of Sabah and Sarawak*, recognised only two species, namely *Aulandra longifolia* and *A. beccarii*, placing *A. cauliflora* into synonymy under *A. longifolia*, as had been suggested as a possibility by van Royen (1958) as more material became available.

Palaquium Blanco, with a total of 120 species (POWO, 2024), primarily has a western Malasian distribution, with the majority of species (around 90%) found on the Sunda shelf. The remaining species occur across South and East Asia to Australasia.

The morphological similarities between *Aulandra* and *Palaquium* have long been recognised. When Lam (1927) first described *Aulandra*, he placed it in a group together

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with *Palaquium* based on the similarity of floral characters (primarily the presence of hexamerous calyx and corolla lobes) but noting the distinctions of a staminal tube and “very large seed-scar” in *Aulandra*. He used terminologies and rank names in his classification system that conflict with modern usage (e.g. he placed *Aulandra* and *Palaquium* together in a ‘division’), but nevertheless, his concepts of relationships are clear. This close relationship was also retained by Aubréville (1964) in tribe Palaquieae within the subfamily Madhucoideae. Pennington (1991) observed that *Aulandra* is “closely related to *Palaquium* but differing from it in its cauliflory or ramiflory, the perennial densely scaly inflorescence axes, and the united filaments”. Chai & Yii (2002) also confirmed the close relationship between the two genera, stating that *Aulandra* could be distinguished by its “cauliflorous or ramiflorous habit, flowers that are borne terminally on a brachyblast and by the filaments which are fused for about half of their length or more into a staminal tube”; indeed, the name of the genus *Aulandra* relates to the staminal tube (Greek: *aulos* = ‘tube’ and *anēr* = ‘male’; Lam, 1927).

The first molecular evidence of the strong affinity between the two genera was published by Gautier *et al.* (2013) and by Richardson *et al.* (2014), where ITS data showed *Aulandra longifolia* (the type species of the genus) nested in *Palaquium*. This nesting of *Aulandra longifolia* was also confirmed, with maximum phylogenetic support, in a recent *Palaquium* study using target capture data (Phang *et al.*, 2023).

Materials and methods

Three new herbarium specimen accessions representing all three *Aulandra* species as currently recognised by POWO (2024) and WFO (2024) were added to the sampling in Phang *et al.* (2023), bringing the total matrix to 89 sequences representing 19 taxa (Supplementary file 1). Laboratory and bioinformatic methods follow Phang *et al.* (2023), except for genomic extraction of the *Aulandra beccarii* and *A. cauliflora* accessions (sampled from type specimens held in the Kew herbarium), which was carried out according to the Basic Protocol 1 described by Latorre *et al.* (2020), following precautions described by Ferrari *et al.* (2023). For phylogenomic analysis, the specific method (iii) in Phang *et al.* (2023) was reapplied to the increased sampling, where the monophyletic outgroup approach in Yang & Smith (2014) was used to produce a concatenated supermatrix to generate a maximum-likelihood tree.

Results

All *Aulandra* species form a clade nested in the main *Palaquium* clade with maximum support (bootstrap value [BS] = 100) and including the type species of the genus (*A. longifolia*), type material of *A. cauliflora*, and type material of *A. beccarii* (Figure 1, Supplementary File 2 [full tree]; but see the notes under new species below). *Aulandra*

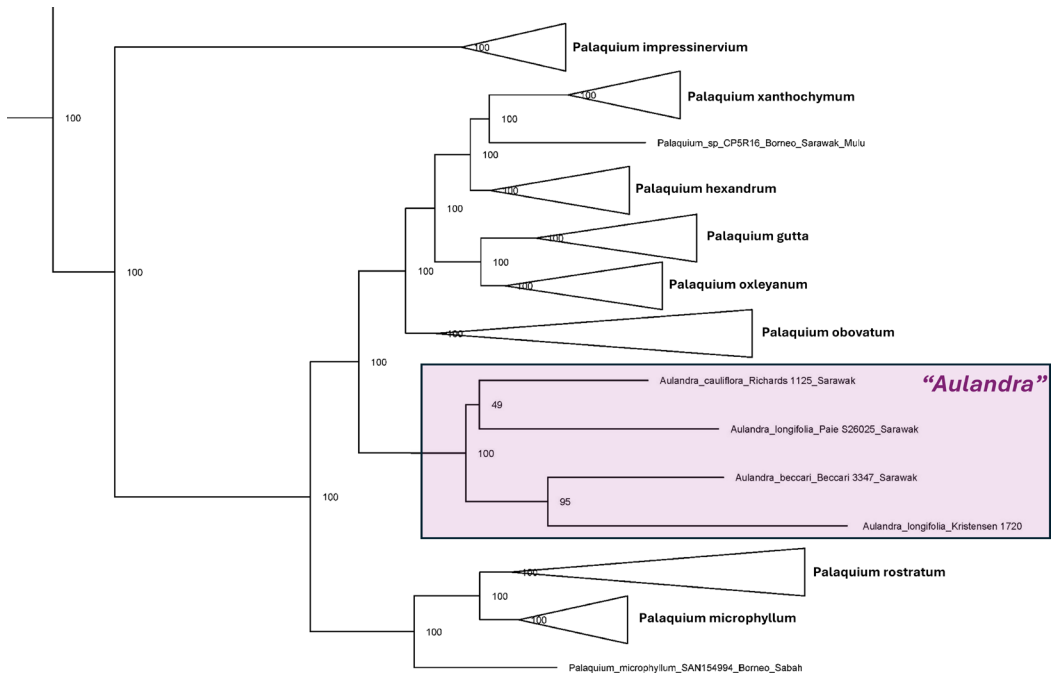


Figure 1. Maximum-likelihood tree of *Aulandra* species in relation to *Palaquium* species sampled in Phang *et al.* (2023), based on concatenated loci from the custom bait-set. Bootstrap values are indicated at each node.

cauliflora formed a weakly supported (BS = 49) clade with an *A. longifolia* sample (Paie S26025(E)), which was sister to another strongly supported (BS = 95) clade containing type material of *A. beccarii* and a sample of *A. longifolia* (Christenson 1720 (K); taken from the Kew Plant and Fungal Tree of Life [Baker *et al.*, 2022] and also included in Phang *et al.* (2023).

Discussion

Our results provide strong support for the inclusion of *Aulandra* in *Palaquium*. All accessions of *Aulandra* in this investigation and in previous molecular studies (Gautier *et al.*, 2013; Richardson *et al.*, 2014; Phang *et al.*, 2023) are nested in *Palaquium*.

Morphologically, the characters separating *Aulandra* from *Palaquium* have traditionally been the seed scar covering more than half the seed surface (vs seed scar covering less than half the seed surface), the cauliflorous or ramiflorous fascicles on scaly brachyblasts (vs axillary fascicles without scaly brachyblasts), and the presence of a staminal column (vs stamens being free) (Lam, 1927; van Royen, 1958, 1960; Pennington, 1991). When reviewing these characters across *Palaquium* species, the width of the seed scar is recorded in the literature as being highly variable, which leaves cauliflory and the staminal

column as the only characters defining *Aulandra*. However, van Royen (1960) noted that *Palaquium ellipticum* (Dalzell) Baill. has filaments “almost entirely united with each other and the corolla”, while *Palaquium xanthochymum* (de Vriese) Pierre ex Burck is said to have “stamens 12, some or all cohering at their base”. Although cauliflory is not documented in Malesian species of *Palaquium*, it is recorded as a variable feature in Sapotaceae, such as within *Planchonella* (Munzinger & Swenson, 2009) and *Pradosia*, where cauliflory has evolved at least twice in the latter genus (Terra-Araujo et al., 2015). In view of these overlapping features, the morphological support for keeping the genera separate appears weak and does not conflict with the robust molecular support for their synonymisation.

Relationships between species are, however, unclear: *Aulandra cauliflora* forms a clade with an accession of *A. longifolia* (Paie S26025), while the accession of *A. beccarii* (Beccari 3347) forms a clade with another accession of *A. longifolia* (Christensen 1720). The Christensen 1720 specimen has only fruit, and its identification could not be verified without the diagnostic floral characters. Beccari 3347 is the only known collection of *Aulandra beccarii*. Increased sampling, especially of flowering material, is needed to help clarify species circumscriptions. While we recognise the equivocal results in the molecular data available, we find that morphological overlaps between *Aulandra longifolia* and *A. cauliflora*, recognised by van Royen (1958), justify the synonymisation of the latter into *A. longifolia* by Chai & Yii (2002). However, the sharp distinction in the number of secondary veins between the non-flowering Christensen 1720 specimen (34–37 pairs), and the Beccari 3347 collection (9–15 pairs), a character used by van Royen (1958) to distinguish species of *Aulandra*, leads us to retain *A. beccarii* as a separate species until more material becomes available.

Here we make the combination for *Aulandra longifolia* in *Palaquium*. This study has, however, also revealed nomenclatural complexity regarding the correct application of the name *Aulandra beccarii*, which has necessitated the description of a new species.

Taxonomic treatment

Palaquium Blanco, Fl. Filip. 403 (1837). – Type species: *Palaquium lanceolatum* Blanco
Aulandra H.J.Lam, Bull. Jard. Bot. Buitenzorg ser. 3, 8: 384, 415 (1927). – Type species:
Aulandra longifolia H.J.Lam (= *Palaquium longifolium* (H.J. Lam) A.Phang)

Palaquium aulandrum A.Phang, sp. nov. – Type: [Malaysia], Borneo, Sarawak, Gunung Balang, Batang-Lupar, Beccari 3347 (holotype FI [FI008956]; isotypes FI [FI008956], G [G00439184], K [K00077764], L [L0006112], P [P00640328]).

Aulandra beccarii auct. non (Pierre ex Dubard) P.Royen: Royen, Blumea Suppl. 4: 263 (1958), p.p.

Most similar to *Palaquium longifolium* (H.J. Lam) A.Phang in the cauliflorous inflorescence, but differs in the smaller leaves (170–300 × (50–)75–95 mm in *Palaquium*

aulandrum, 320–970 × 72–280 mm in *P. longifolium*) and fewer secondary veins (9–15 pairs in *P. aulandrum*, 22–37 pairs in *P. longifolium*).

Tree, size unknown. *Twigs* rugulose to rugose, 2–5 mm in diameter, reddish brown tomentose, glabrescent. *Leaves* loosely clustered; stipules lanceolate, up to 1.5 mm long, outer surface reddish brown tomentose, inner surface glabrous, caducous; petiole flat above, 15–35 mm long, thickened and rugose at base, reddish brown tomentose, glabrescent; blade coriaceous, oblong-obovate to elliptic, apex acuminate, base decurrent along petiole, 170–300 × (50–)75–95 mm, glabrous above and below; midrib slightly raised or prominent above, raised below, secondary veins 9–15 pairs, ascending at an angle of 50° to 60°, straight or slightly curved, diminishing until inconspicuous near blade margins, impressed above, prominent below, tertiary veins, transverse, inconspicuous above, faint below. *Inflorescences* fascicles, cauliflorous. Flowers borne on vermiform brachyblasts up to 11 mm long; bracts deltate, up to 1.5 mm long, outer surface reddish brown tomentose, inner surface glabrous; pedicels angular, 2–6 mm long, reddish brown tomentose. *Sepals* 6, outer sepals ovate, 2.5–3 × 2–2.5 mm, outer surface reddish brown tomentose, inner surface glabrous, margins fimbriate, inner sepals elliptic-ovate, slightly smaller than the outer ones, outer surface reddish brown or greyish tomentose, glabrous towards margin, keeled, inner surface glabrous, margins fimbriate. *Corolla* (in bud only) up to 3 mm long, lobes oblong, c.2.5 × 1 mm, glabrous outside and inside. *Stamens* 18, in 3 rows, anthers cordate-sagittate, 1–1.5 mm long, acute, acumen bifurcate or emarginate, hirsute; filaments broadly subulate, united, c.0.3 mm long, glabrous. *Ovary* conoid, up to 1 mm long, reddish brown tomentose, glabrous at base. *Style* subulate, c.2 mm long, with 6 longitudinal grooves, glabrous except for scattered hairs at the apex. *Fruit* unknown. *Seed* unknown.

Distribution. Recorded from only a single location: Gunung Balang, Batang-Lupar, in Sarawak, Malaysia.

Habitat and ecology. Although the exact coordinates of the original collection are not known, Batang Lupar is a significant river in Sarawak within Sri Aman Division, with a navigable length of around 105 km (65 miles), through areas of tropical rain forest with some hilly areas with altitudes up to 700 m. Flowering specimens were found in April.

Etymology. The epithet *aulandrum* is given to reflect the species' former placement in the genus *Aulandra*.

Proposed IUCN conservation category. The species is globally assessed as Critically Endangered (Julia, 2021; as *Aulandra beccarii*), being rare and endemic, recorded from only a single location in Sarawak, thus having an extremely restricted area of occurrence (4 km²) and similarly limited extent of occurrence. Population reduction is estimated to be severe (> 80%) due to various consequences of deforestation, land use and habitat loss.

Notes. The type of *Aulandra beccarii* is the collection *Teysmann* H.P. 5068 (P [P00645625]; [Figure 2A](#)), as this is the only collection mentioned in the protologue of the basionym, *Palaquium beccarii* Pierre ex Dubard (Dubard, 1909). However, the specimen in Paris was determined by Lam in 1938 as the distantly related *Palaquium dasyphyllum* Pierre ex Dubard. With this determination of *Teysmann* H.P. 5068, it means that *Palaquium beccarii* is the same species as *P. dasyphyllum*. Although *Palaquium dasyphyllum* was based on the illegitimate name *Isonandra dasyphylla* de Vriese, which is a later homonym of *Isonandra dasyphylla* Miq., Art. 58.1 of the Shenzhen Code (Turland et al., 2018) means that *P. dasyphyllum* must be treated as a replacement name with the same type as the illegitimate name. *Palaquium dasyphyllum* Pierre ex Dubard has hitherto mostly been treated as having the basionym *Isonandra dasyphylla* De Vriese from 1860, meaning that it would have priority over *P. beccarii* from 1909. However, as *Isonandra dasyphylla* De Vriese is illegitimate, *Palaquium dasyphyllum* and *P. beccarii* have equal priority from 1909. We here establish the priority of *Palaquium dasyphyllum* over *P. beccarii*.

Specimens examined. Known only from the type specimens.



Figure 2. Specimen images of collections obtained from Muséum national d'Histoire naturelle, Paris (France): A, *Teysmann* 5068 [P00645625], holotype of *Palaquium beccarii* (<http://coldb.mnhn.fr/catalognumber/mnhn/p/p00645625>); B, *Beccari* 3347 [P00640328] (<http://coldb.mnhn.fr/catalognumber/mnhn/p/p00640328>). Images: Muséum national d'Histoire naturelle, Paris (France).

Palaquium dasyphyllum Pierre ex Dubard, Bull. Soc. Bot. France 56 (Mém. 16): 8 (1909).

– *Isonandra dasyphylla* de Vriese in Natuurk. Tijdschr. Ned.-Indië 21: 307 (1860), nom. illeg. non Miq. (1852). – Type: Borneo, [Kalimantan], Banjarmasin, *Teysmann* H.P. 5066 (holotype P [P00645624]).

Palaquium beccarii Pierre ex Dubard, Bull. Soc. Bot. France 56 (Mém. 16): 20 (1909). – Type: Borneo, *Teysmann* H.P. 5068 (holotype P [P00645625]), **syn. nov.**

Notes. There is a second collection in the Paris herbarium (*Beccari* 3347 [P00640328]; [Figure 2B](#)) labelled with the name *Palaquium beccarii* that is not cited in the protologue. Confusion arose when van Royen (1958) made the new combination *Aulandra beccarii* and wrongly cited the type as *Beccari* 3347. The combination is valid and legitimate but applies to the species that is typified by *Teysmann* H.P. 5068 (see [Figure 2A](#)), which has now been identified as *Palaquium dasyphyllum*. This leaves the species that includes *Beccari* 3347 (hitherto known as *Aulandra beccarii*) without a name. As changing the type is not permitted without a conservation proposal, and as these are relatively unknown species for which a conservation proposal may not be appropriate, we prefer to describe it here under the name *Palaquium aulandrum*.

When van Royen (1958) transferred *Palaquium beccarii* to *Aulandra*, he provided a description based on the collection *Beccari* 3347. We have verified and adapted van Royen's description as well as the description in the *Tree Flora of Sabah and Sarawak* (Chai & Yii, 2002) and given the type as *Beccari* 3347, the only known collection of this species, in order to validly publish the species with a different name in the sense that van Royen intended. As 'beccarii' is not available for the epithet of a new species in *Palaquium*, the new epithet 'aulandrum' is given to reflect the species' former placement in the genus *Aulandra*.

Palaquium longifolium (H.J. Lam) A.Phang, **comb. nov.** – *Aulandra longifolia* H.J.Lam, Bull. Jard. Bot. Buitenzorg, sér. 3, 8: 415, f. 6 (1927). – Type: Borneo, [Kalimantan], Loembis, *Amdjah* 238 (lectotype L [L0006113], designated by van Royen (1958); isoelectotypes BO [BO-1359858, BO-1359859, BO-1359860]).

Aulandra cauliflora H.J.Lam, Hooker's Icon. Pl. 34: t. 3360 (1938). – Type: [Malaysia], Sarawak, IVth Division, Near Long Kapa, Mount Dulit (Ulu Tinjar), *Richards* 1125 (holotype K [K000777765, K000777766]).

Notes. The holotype of *Aulandra cauliflora* is mounted over two sheets which are clearly labelled as Sheet 1 and Sheet 2 of the same specimen, hence constituting a single specimen under Article 8.3 of the Shenzhen Code (Turk et al., 2018).

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Supplementary material

Supplementary file 1. List of accessions sampled in this study with voucher information (*newly sampled accession). Herbaria acronyms follow Thiers ([continuously updated](#)).

Supplementary file 2. Full (uncollapsed) maximum-likelihood tree of *Aulandra* species in relation to all samples in Phang *et al.* (2023), based on concatenated loci from the custom bait-set. Bootstrap values are indicated at each node.

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