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A revised generic circumscription of *Exocarpos* (Santalaceae), including the transfer of *Omphacomeria* to *Exocarpos*

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Introduction

Santalaceae (*sensu lato*, including Viscaceae) is a family of parasitic plants with 43 genera and c. 1115 species according to Plants Of the World Online (POWO, Govaerts *et al.* 2021, continuously updated). All genera currently recognized in POWO were included in a molecular phylogenetic study by Der and Nickrent (2008), with a few exceptions. They did not include the New Caledonian genus *Elaphanthera* N.Hallé (monotypic) that they considered a synonym of *Exocarpos* Labill., the south-east Asian *Henslowia* Blume (three species) that they considered a synonym of *Dendrotrophe* Miq., the Malesian *Hylomyza* Danser (three species) that they considered a synonym of *Dufrenoya* Chatin, or the southern African *Lacomucinaea* Nickrent & M.A.García (monotypic) that was later segregated from *Thesium* L. (Nickrent & García 2015).

In this study, the sampling of Santalaceae conducted by Der and Nickrent (2008) was expanded, particularly with regard to New Caledonian species, in order to clarify the relationship between *Elaphanthera* and *Exocarpos*. The monotypic genus *Elaphanthera* was established by Hallé (1988) to accommodate *Exocarpos baumannii* Stauffer (1959), a species restricted to the ultramafic substrates of the main island of New Caledonia. *Exocarpos* encompasses c. 27 species according to POWO,

Abstract

A molecular phylogenetic study was conducted to clarify the relationships between three genera of Santalaceae, the mostly Oceanic *Exocarpos* Labill., the Australian endemic and monotypic *Omphacomeria* (Endl.) A.DC., and the monotypic *Elaphanthera* N.Hallé, endemic to the main island of New Caledonia. *Omphacomeria acerba* (R.Br.) A.DC. was found to be nested in *Exocarpos*, while *Elaphanthera baumannii* (Stauffer) N.Hallé was sister to *Exocarpos*. Placement of *Elaphanthera* and *Omphacomeria* in an expanded *Exocarpos* is proposed on the basis of molecular data, supported by morphology. A new combination, *Exocarpos acerbus* (R.Br.) Lepschi, *comb. nov.*, is provided to accommodate *Omphacomeria acerba* in *Exocarpos*.

Keywords: Australia, New Caledonia, parasitic plants, taxonomy, ultramafic

occurring in south-east Asia, Malesia, Australia, and the Pacific Islands, extending to New Zealand, Hawai'i and French Polynesia. The monotypic Australian genus *Omphacomeria* (Endl.) A.DC. was also included in this analysis, in order to examine the relationship of this genus to *Exocarpos*, to which *Omphacomeria* is putatively closely related (Stauffer 1959; Nickrent *et al.* 2010). In two previous phylogenetic studies of the Santalaceae or Santalales, *Omphacomeria* has been retrieved as sister to *Exocarpos* (Der & Nickrent 2008) or even nested in this genus (Su *et al.* 2015). Stauffer (1959) considered that another genus, *Anthobolus* R.Br., was closely allied to *Exocarpos* and *Omphacomeria*. However the molecular phylogenetic analysis by Der & Nickrent (2008) recovered this genus within Opiliaceae. Kuijt & Hansen (2015) rejected this new placement and maintained *Anthobolus* in Santalaceae. Nevertheless, a later molecular study (Nickrent *et al.* 2019) based on a different accession of *Anthobolus* confirmed its placement within Opiliaceae and the genus is therefore not discussed further here.

Methods

Samples of *Elaphanthera baumannii* (Stauffer) N.Hallé, *Exocarpos neocalaedonicus* Schltr. & Pilg., *Exocarpos phyllanthoides* Endl., and *Exocarpos pseudocasuarina* Guillaumin were obtained from the field and from the Herbarium of New Caledonia (NOU, Bruy *et al.* 2023). Total genomic DNA was extracted from silica-dried leaves (Chase & Hills 1991) following a modified cetyltrimethylammonium bromide (CTAB) protocol (Doyle & Doyle 1987).

Nuclear small subunit (SSU) rDNA and two plastid genes were amplified: maturase K (*matK*) and ribulose-1,5-bisphosphate carboxylase/oxygenase large subunit (*rbcl*) with primers designed by Rogers *et al.* (2008). Purification and bidirectional sequencing were carried out by an external service (Genoscreen, Lille, France) on an automated sequencer using BigDye Terminator V3.1 reagents. The sequences were edited in MEGA X (Kumar *et al.* 2018). The dataset also included previously published accessions of *Exocarpos*, one representative of each genus of the *Santalum* clade (*sensu* Der & Nickrent 2008) to which *Exocarpos* belongs, as well as the genera *Leptomeria* R.Br., *Mida* R.Cunn. ex A.Cunn., *Nanodea* Banks ex C.F.Gaertn., and *Thesium* as further outgroups.

Sequences were aligned using MUSCLE (Edgar 2004) and cleaned from problematic alignment blocks using Gblocks 0.91 (Castresana 2000) using the less stringent options set.

Phylogenetic analyses were conducted using Bayesian inference. The best substitution models for each DNA regions were determined using jModelTest version 2.1.6 (Darriba *et al.* 2012) and Akaike's information criterion (AIC). Then, these models were used in MrBayes v. 3.2.7 (Ronquist & Huelsenbeck 2003) linking the branch lengths but not the sampling of character-state frequencies, substitution rates, the gamma shape parameter and the proportion of invariant sites. Markov chain Monte Carlo (MCMC) analysis were performed for one million generations with eight chains, sampling every 1000th generation. Convergence of runs was assessed by examining the ESS of parameters under Tracer v.1.7 (Rambaut *et al.* 2018), using the recommended threshold of 200 (Drummond *et al.* 2006). A generated majority-rule consensus tree was generated after discarding a burn-in fraction of 25%. The tree was rooted with *Thesium*.

Results

A combined matrix of 22 terminals and 4,251 sites (with 14 % of gaps) was analysed. In our Bayesian phylogenetic analyses, convergence of runs is obtained with all parameters ESS values ≥ 200 . In the majority-rule consensus tree focused on *Exocarpos s.l.* (Figure 1) inferred from SSU rDNA, *matK* and *rbcl*, the genus *Exocarpos* was paraphyletic with the monotypic *Omphacomeria* nested in it, while *Elaphanthera baumannii* was recovered as sister taxon with strong support (PP=1).

Discussion

With our current sampling, *Elaphanthera baumannii* is retrieved as sister to the rest of the genus *Exocarpos*. Our results concur with the original placement of this species in *Exocarpos* by Stauffer (1959), and the conclusion of Der and Nickrent (2008) who treated *Elaphanthera* as a synonym of *Exocarpos*. *Elaphanthera* is also not included as an accepted taxon in the treatment of Santalaceae by Kuijt and Hansen (2015). *Elaphanthera* was defined by Hallé (1988) by the following morphological characters:

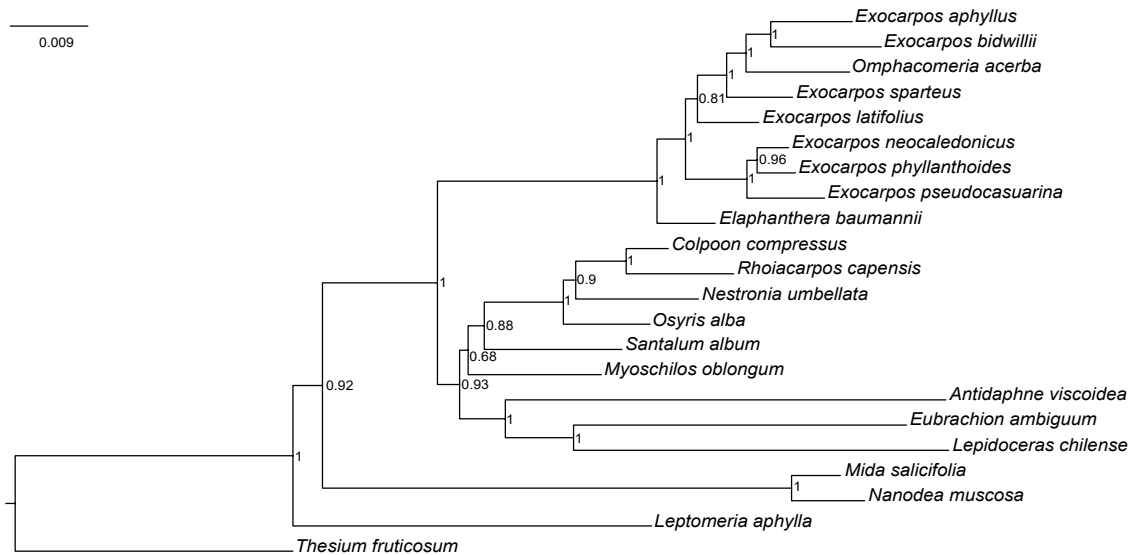


Figure 1. Majority-rule consensus tree of Santalaceae with a focus on *Exocarpos s.l.* resulting from Bayesian analysis of three DNA regions: nuclear small-subunit ribosomal DNA, *rbcl* and *matK*. Support values at nodes refer to posterior probabilities (PP).

opposite or decussate phyllotaxy (vs. alternate in *Exocarpos*); anthers deeply cleft between the thecae (vs. shallowly cleft); floral disc with shield-like scutellae on the lobes (vs. scutellae absent); and prominently longitudinally ridged fruit (vs. +/- smooth fruit). We consider that these characters serve to define a taxon (*Exocarpos baumannii*) at the rank of species, rather than supporting a distinction at the generic level. Characters such as the degree of cleavage between the anther thecae and relative prominence of fruit ornamentation (both of which are particularly well developed in *Ex. baumannii*, but less so in other species of *Exocarpos*), are part of a continuum of variation in these characters within the genus *Exocarpos*. Opposite and/or decussate phyllotaxy also occurs in the Australian alpine species *Ex. nanus* Hook.f. The presence of scutellae on the lobes of the floral disc in *Ex. baumannii* is otherwise unknown elsewhere in the genus *Exocarpos*, however this single character is not considered sufficient to warrant recognition at generic rank.

Omphacomeria is nested in the genus *Exocarpos* in our analysis, a result congruent with a previous study (Su et al. 2015) and ongoing phylogenomic investigations in the Santalales based on target sequence capture data for >300 loci (B.M. Anderson, pers. comm.). On the basis of these results and morphology, we propose placing

Omphacomeria in synonymy of *Exocarpos*. With the inclusion of *Omphacomeria*, *Exocarpos sensu* Stauffer is rendered monophyletic. The close relationship between *Omphacomeria* and *Exocarpos* has been noted previously (Der & Nickrent 2008; Su et al. 2015), but the relationship between these taxa does not appear to have been explicitly tested with greater taxon sampling. Stauffer (1959 p. 83) argued that *Omphacomeria* was misplaced in the tribe Osyridae, and included it in his concept of Anthoboleae, noting the morphological congruence between *Omphacomeria* and *Exocarpos* ("Es seien hier nochmals die hauptsachlichsten Kritirien zusammengefasst, die zu der Transferierung von *Omphacomeria* fuhrten: Achsenbau wie *Exocarpos*, Pollenbau wie *Exocarpos*, Staminabau und Fehlen der Postaminalhaare wie bei *Exocarpos*, Placentation wie bei *Exocarpos*"), but retained *Omphacomeria* as a monotypic genus without further comment. Subsequent treatments of *Omphacomeria* (George 1984; Wiecek 1992; Jeanes 1999; Nickrent et al. 2010; Kuijt & Hansen 2015) have not considered generic limits.

Omphacomeria has been distinguished from *Exocarpos* by the following morphological characters: plants unisexual (vs. mostly bisexual in *Exocarpos*, but see discussion below); ovary inferior (vs. superior, but see discussion below); and fruit sessile (vs. fruit borne

on a fleshy, greatly expanded receptacle). As with *Elaphanthera*, we consider that these characters serve to define a taxon (*Exocarpos acerbus*) at species rank, rather than supporting a distinction at the generic level.

Omphacomeria is dioecious, and while flowers in the Santalaceae are usually bisexual (Kuijt & Hansen 2015), sexual expression in the genus *Exocarpos* s.s. (excluding *Omphacomeria*), is diverse and frequently unclear, with bisexual, androdioecious, dioecious, and possibly also monoecious and gynodioecious systems occurring (Stauffer 1959). While dioecy is unusual among Australian Santalaceae and can aid in distinguishing *Omphacomeria* from other Australian members of the family, this sexual system has also been recorded in at least one Australian species of *Exocarpos*, *E. strictus* R.Br., as well as in *E. micranthus* Stauffer from New Guinea, and *E. phyllanthoides* Endl. from New Caledonia and Norfolk Island (Stauffer 1959). Accordingly, sexual system is not considered to be a useful distinguishing character to support recognition of *Omphacomeria* at generic rank.

Similarly, ovary position in *Omphacomeria*, described as inferior (de Candolle 1857; George 1984; Wiecek 1992; Jeanes 1999) or “practically inferior” (Smith & Smith 1943), is not clearly distinguishable as a morphological state from that observed in the genus *Exocarpos*, which appears transitional between truly inferior and superior states, and is therefore unreliable as a generic character. The ovary in *Exocarpos* is described as “semi-inferior” by Kuijt and Hansen (2015), and Smith and Smith (1943) describe the ovary in *Exocarpos* as “partly inferior though it appears to be essentially superior” and “not nearly as superior as it appears since the ventral carpellary strands arise deep in the fleshy receptacle that bears the ovary”.

The fruit in *Exocarpos* s.s. (excluding *Omphacomeria*) is borne on a brightly coloured, fleshy receptacle, and this character is absent in *Omphacomeria*. Fruits in *Exocarpos* s.s. are +/- hard when ripe, due to a comparatively thin mesocarp, and the exocarp is generally dark or dull coloured (dark green to purplish), often contrasting strongly with the receptacle colour. In *Omphacomeria*, the fruit is sessile, fleshy, with a thicker mesocarp and a dull green exocarp, frequently suffused purplish. The development of a brightly coloured, fleshy receptacle in *Exocarpos* s.s. is clearly related to fruit dispersal, predominantly by birds (Stauffer 1959; Barker & Vestjens 1989, 1990). Fruit dispersal vectors for *Omphacomeria*

(= *Exocarpos acerba*) are unknown, but the nature of the fruits also suggests bird dispersal, despite their relatively dull coloration. Birds (e.g. Emus, *Dromaius novaehollandiae*) are known to consume fruits of other species of Australian Santalaceae with dull, greenish fruits, such as *Choretrum pauciflorum* R.Br. (K.L.Brown, pers. comm.) and *E. sparteus* R.Br. (Stauffer 1959). The absence of a fleshy receptacle in *Omphacomeria* (= *Exocarpos acerba*) is unique in the genus *Exocarpos*, however this single character is not considered sufficient to warrant recognition at generic rank.

Taxonomy

Only names relevant to this study are presented below. For additional synonymy, see Stauffer (1959) and the Australian Plant Census (<https://biodiversity.org.au/nsl/services/search/taxonomy>; accessed 15 September 2023).

***Exocarpos* Labill., nom. cons., Voy. Rech. Pérouse 1: 155, t. 14 (1800)**

Type: *Exocarpos cupressiformis* Labill.

= *Leptomeria* sect. *Omphacomeria* Endl., *Gen. Pl.* 236 (1837). *Omphacomeria* (Endl.) A.DC., *Prodr. [A. P. de Candolle]* 14(2): 680 (1857), **syn. nov.**

Type (designated by Stauffer 1959): *Omphacomeria acerba* (R.Br.) A.DC.

= *Elaphanthera* N.Hallé, *Fl. Nouv.-Calédonie & Dépend.* 15: 134 (1988).

Type: *Elaphanthera baumannii* (Stauffer) N.Hallé.

***Exocarpos acerbus* (R.Br.) Lepschi, comb. nov.**

Leptomeria acerba R.Br., *Prodr. Fl. Nov. Holland.* 354 (1810). *Omphacomeria acerba* (R.Br.) A.DC., *Prodr. [A. P. de Candolle]* 14(2): 681 (1857).

LECTOTYPE (designated by Stauffer 1959): AUSTRALIA, 1802, Brown 3202 (BM001010, isolecto K, both n.v.).

<https://www.ipni.org/n/77327203-1>

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and advice on sequencing. One anonymous reviewer provided insightful comments on a previous version of the manuscript. The authors declare no conflicts of interest.

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Appendix

Genbank accession numbers for the three loci: nuclear small-subunit ribosomal DNA, *rbcL* and *matK*. Newly produced sequences are shown in bold.

Antidaphne viscoidea Poeppig & Endlicher, Costa Rica, S.Sargent *s.n.* (SIU), L24080, L26068, EF464500. *Colpoon compressum* Berg., South Africa, D.L.Nickrent, K.Steiner & A.Wolfe 4084 (SIU), EF584574, EF584590, EF584616. *Elaphanthera baumannii* (Stauffer) N.Hallé, New Caledonia, Y.Pillon *et al.* 1484 (NOU), **OR731824**, **OR594625**, **OR731824**. *Eubrachion ambiguum* (Hooker & Arnott) Engler, Puerto Rico, D.L.Nickrent, D.Clark & P.Clark 2699 (SIU), L24141, L26071, EF464498. *Exocarpos aphyllus* R.Br., Australia, A.Markey *s.n.* (SIU), EF584575, EF584593, EF584618. *Exocarpos bidwillii* Hook., New Zealand, B.Molloys *s.n.* (SIU), L24142, EF584594, EF584619. *Exocarpos latifolius* R.Br., Australia, A.Shapcott *s.n.* (BRI), —, KF496569, KM894916. *Exocarpos neocaledonicus* Schltr. & Pilg., New Caledonia, Y.Pillon *et al.* 1482 (NOU), 1482, —, **OR594626**, **OR594622**. *Exocarpos phyllanthoides* Endl., New Caledonia, Y.Pillon 1494 (NOU), **OR731825**, **OR594627**, **OR594623**. *Exocarpos pseudocasuarina* Guillaumin, New Caledonia, Y.Pillon *et al.* 1483 (NOU), **OR731826**, **OR594628**, **OR594624**.

Exocarpos sparteus R.Br., Australia, A.Markey *s.n.* (SIU), MH390518, MH390686, MH390644. *Lepidoceras chilense* (Molina) Kuijt, Chile, C.Martcorena & R.Rodríguez 10043 (CONC), EF464459, MH390687, MH390645. *Leptomeria aphylla* R.Br., Australia, B.J.Lepschi & A.J.Whalen 4875 (CANB), MH390526, MH390694, MH390651. *Mida salicifolia* A.Cunn., New Zealand, C.C. Ogle 3413 (CANB), EF584577, MH390691, MH390649. *Myoschilos oblongatum* Ruíz & Pavón, Argentina, R.Vidal-Russell *s.n.* (SIU), EF584578, MH390688, MH390646. *Nanodea muscosa* Banks ex C.F.Gaertn., Argentina, L. Collado *s.n.* 4893 (SIU), EF584579, MH390692, MH390650. *Nestronia umbellula* Raf., USA, L.J. Musselman *s.n.* (SIU), MH390521, MH390689, MH390647. *Omphacomeria acerba* (R.Br.) A.DC., Australia, B.J. Lepschi & B.R. Murray 4213 (CANB), EF584580, EF584602, EF584627. *Osyris alba* L., Spain, D.L.Nickrent, A.Aparicio & I.Sanchez García 4062 (SIU), —, LT599649, AM396499. *Rhoiacarpus capensis* A.DC., South Africa, D.L.Nickrent & G.Marx 4117 (SIU), EF584584, EF584606, EF584630. *Santalum album* L., India, R. Narayana *s.n.* (no voucher), L24416, —, —. *Santalum album* L., China, X.Liu *s.n.* (CAF), —, MW464922, MW464922. *Thesium fruticosum* A.W.Hill, South Africa, D.L.Nickrent & E.Brink 4115 (SIU), EF584587, EF584609, EF584633.