From the Mediterranean to the Pacific: re-circumscription towards *Notelaea s.l.* and historical biogeography of a generic complex within Oleinae (Oleaceae)

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ABSTRACT

Tackling the complicated infrafamilial classification of the economically important Oleaceae requires a piecemeal approach that addresses generic circumscriptions. Here, focusing on the distinct clade formed by the generic complex *Nestegis*, *Notelaea*, *Osmanthus*, *Phillyrea*, and *Picconia* within the subtribe Oleinae, we aim to elucidate their boundaries and relationships and to evaluate their biogeographic history in light of their peculiar disjunct distribution in the Macaronesian, Mediterranean, and Pacific Regions. Based on phylogenomic data from plastid and nuclear DNA of an extensive sampling, the results show six subclades within this generic complex, which are also geographic segregates found in Australia (*Notelaea*), Hawaiian Islands (*Nestegis sandwicensis*), Macaronesia (*Phillyrea* and *Picconia*), Mediterranean Region (*Phillyrea*), New Caledonia (*Osmanthus* section *Notosmanthus*), and New Zealand (*Nestegis s.s.*). Accounting for broad morphological overlaps within this clade, we recognize three genera (*Phillyrea*, *Picconia*, and *Notelaea s.l.*), subsuming all Pacific taxa under *Notelaea s.l.* Molecular dating and biogeographic analyses indicate that this clade originated in Eurasia during the Early Miocene (mean 23.2 Mya, 95% HPD: 23.8 – 14.7). Finally, dispersal (rather than continental vicariance) is likely the main explanation for the global, disjunct distribution of this group; with island-hopping and local extinction as the hallmarks of its evolutionary history.

ADDITIONAL KEYWORDS: Azores - Canary Islands - Madeira - morphology - museomics - Nestegis - Osmanthus - Phillyrea - Picconia - Zealandia

INTRODUCTION

Despite its moderate size, with ca. 700 species in 28 genera, and its economic importance, the Oleaceae remain a taxonomic conundrum. After the seminal work by Wallander & Albert (2000), that reorganized the family into five well-defined tribes (namely Fontanesieae, Forsythieae, Jasmineaee, Myxopyreae, and Oleeae), subsequent molecular studies, mostly at the generic level, invariably revealed much of its complexity, notably an extensive paraphyly and polyphyly (Li, Alexander & Zhang, 2002; Lee *et al.*, 2007; Besnard *et al.*, 2009; Yuan *et al.*, 2010; Guo *et al.*, 2011; Hong-Wa & Besnard, 2013; Jeyarani *et al.*, 2018; Olofsson *et al.*, 2019; Dupin *et al.*, 2020; Li *et al.*, 2020; Dong *et al.*, 2022). Oleinae, the largest subtribe within the largest tribe, Oleeae, exhibits the most instances of polyphyly within its currently recognized 15 genera (Table 1), particularly in *Chionanthus* L. (Besnard *et al.*, 2009; Yuan *et al.*, 2010; Guo *et al.*, 2011; Hong-Wa & Besnard, 2013; Olofsson *et al.*, 2019; Dupin *et al.*, 2020).

Yet, current knowledge also supports the recognition of a few, well-defined clades, which allows for a stepwise taxonomic delineation. One such clade, which is the focus of this paper, comprises members of the genera *Nestegis* Raf. (Rafinesque, 1838), *Notelaea* Vent. (Ventenat, 1804), *Osmanthus* Lour. section *Notosmanthus* P.S.Green (Green, 1963), *Phillyrea* L. (Linnaeus, 1753), and *Picconia* A.DC. (De Candolle, 1844). Given the peculiar distribution of this clade in the Macaronesian, Mediterranean, and Pacific Regions, it will be referred to hereafter as the MMP clade. This distinct clade within Oleinae, sister to Eurasian *Osmanthus*, has been recovered by multiple works (Guo *et al*., 2011; Olofsson *et al.*, 2019; Dupin *et al.*, 2020), which excludes the possibility of such results being a consequence of a phylogenetic artifact. However, despite the MMP clade's distinctiveness within Oleinae, relationships among its own members, which form a generic complex, have been difficult to unravel likely due to a lack or insufficiency of molecular data and sampling, and an unstable taxonomy.

Taxonomic studies of the MMP clade date back to 1753 (Table 1), with the description of the genus *Phillyrea* by Linnaeus in Species Plantarum. The type species of most of these genera were first described within *Olea* L. (e.g., *Olea apetala* Vahl for *Nestegis*, *Olea fragrans* Thunb. for *Osmanthus*, and *Olea excelsa* Sol. for *Picconia*) and there has been a continuous and frequent transfer of species from one genus to another (e.g., Johnson 1957, 1958, Green, 1968), which all denotes the complexity of this group. Morphologically, members of the MMP clade can be distinguished from *Olea* by their inflorescences that are axillary and mostly racemose-decussate, which are usually terminal and cymose-paniculate in *Olea* (Green, 2004), yet morphological limits are obscure among them. The gradual description of new MMP species over the last century expanded the concept of each genus, rendering any one of them quite heterogeneous and making the classification within the MMP clade arbitrary, barely defined on natural assemblages. Attempts were thus made to clarify boundaries within this generic complex as demonstrated by the works of Johnson (1957) and Green (1958, 1963a,b, 1968), although these authors differed in their approach. Johnson chose a segregated generic concept [e.g., with the resurrection of the genus *Gymnelaea* (Endl.) Spach, which resulted in illegitimate names that were later reconciled within *Nestegis* (Johnson, 1958)], while Green preferred a broad view of genera pending detailed revisions on a world basis, but he also conveniently adopted a geographic perspective for the taxa of the MMP clade [e.g., with the transfer of species from *Nestegis* to the newly circumscribed *Osmanthus* section *Notosmanthus* for New Caledonia and to *Notelaea* for Australia and Tasmania (Green, 1963a,b, 1968)].

As currently circumscribed, the MMP clade comprises 24 species (Table 1). *Osmanthus* section *Notosmanthus* can be distinguished from Eurasian *Osmanthus* by its racemose-decussate inflorescence, undifferentiated style, conical ovary, and smaller fruit vs. an umbellate-fasciculate inflorescence, well-differentiated style, rounded ovary, and slightly larger fruit (Table 2; Green, 1958, 1963a). Previous studies found them to be also phylogenetically distant (Olofsson *et al*., 2019; Dupin *et al*., 2020; Li *et al*., 2020). Therefore, *Osmanthus* section *Notosmanthus* will only be referred to hereafter as 'Notosmanthus' to clearly distinguish it from Eurasian *Osmanthus*. Thus, the five groups within the MMP clade can be distinguished among themselves mostly by floral characteristics such as inflorescence type, aestivation, the presence/absence of petals and their fusion, and the style length (Table 2). However, there is substantial overlap in trait variation and therefore any distinction on morphological grounds seems rather arbitrary. Likewise, all available cytogenetic and nuclear genomic data on species of this clade indicated the same ploidy level [i.e., 2n = (44)-46 chromosomes (Taylor, 1945; Green, 1968; Briggs, 1970; Dawson, 1995; Kiehn, 2005; Yang *et al.*, 2018; Carré *et al.*, 2021)], except one count supporting tetraploidy in an unresolved *Phillyrea* taxon collected in Minorca, Balearic Islands (Cardona, 1991). By contrast, there is quite a clear geographic separation among the five taxa (Table 1), each seemingly having colonized different areas, which perhaps justifies Green's geographic concept (1958, 1963a,b, 1968).

Geographically, the MMP clade is largely Pacific, with one large lineage, comprised of 20 species, distributed quite exclusively among the lands of this region. Indeed, *Nestegis* is largely known from New Zealand and Norfolk Island, although one of its species is native to the isolated Hawaiian archipelago; *Notelaea* occurs only in eastern Australia and Tasmania; and 'Notosmanthus' is restricted to New Caledonia. Two genera, though, are distributed completely outside the Pacific region: *Phillyrea* mainly in the Mediterranean Region, but extending to the Canary Islands with the presence of *P. angustifolia* L. subsp. *canariensis* Rivas Mart. & Del Arco, and *Picconia* in Macaronesia. This geographic distinction among taxa contrasts with a broad morphological overlap making this combination quite unique to this group compared with other Oleaceae; it then highlights the difficulty in rendering an adequate taxonomy within the MMP clade. Additionally, a wide and rather disjunct distribution pattern is not seen in other clades within the family either. In fact, such a distribution pattern is rather rare in plant groups, with *Coriaria* L. (Coriariaceae) being the other known example of a clade with such a disjunct global distribution (Yokoyama *et al*., 2000).

Using phylogenomic data from plastid DNA sequences and three nuclear regions (ribosomal DNA and genes encoding phytochromes B and E), the overall goals of this study are to resolve generic boundaries within the MMP clade and to explore the evolution of its geographic distribution. The resulting phylogenetic tree will serve as a framework for taxonomic realignment and for elucidating the most likely biogeographic region of origin, as well as the directionality and timing of range expansions in the history of this clade.

MATERIALS AND METHODS

TAXON SAMPLING

Our dataset comprised 64 accessions representing 21 out of 24 species of the MMP clade (28 accessions) and about half of the species of Eurasian *Osmanthus* (11 out of 28; 14 accessions). This dataset had all the currently accepted species of *Nestegis*, 'Notosmanthus', *Phillyrea*, and *Picconia*, and most species in *Notelaea* (9 out of 12). For 'Notosmanthus', we included five accessions of *O. austrocaledonicus* (Vieill.) Knobl., representing its infraspecific members, to assess the pertinence of the current taxa delimitation and their identification. We complemented our sampling with the remaining 20 taxa (22 accessions) from other genera within Oleaceae, especially from the Oleeae tribe (Table S1).

MOLECULAR DATASETS

Out of the 64 accessions used here, the data for 61 of them came from GenBank and supplementary materials of previous publications (Olofsson *et al.*, 2019; Dupin *et al.*, 2020). These data are a mix of plastid full genomes, individual plastid markers, sequences from the nuclear ribosomal DNA cluster (nrDNA) at varying lengths (either the full nrDNA cluster or only the ITS region), and partial gene sequences encoding the phytochromes B and E (*phy*B and *phy*E). The addition of two nuclear markers (*phy* genes) to the list of usual markers used for estimating plant phylogenies (chloroplast genes and nuclear ribosomal complex) increases information on sequence divergence (e.g., Dupin *et al*., 2020), and can help deal with speciation, hybridization and incomplete lineage sorting of closely related species.

For the remaining three accessions [for *Chengiodendron matsumuranum* (Hayata) C.B.Shang, X.R.Wang, Yi F.Duan & Yong F.Li, *Phillyrea latifolia* L., and *Picconia excelsa* (Aiton) A.DC.], we used a genome skimming approach to sequence nuclear and plastid genomes. All accessions were sampled from herbarium specimens (from P and TUM). It is worth noting that the *P. excelsa* specimen collected by N. Baudin (1754-1803) was probably collected in Tenerife before his departure for Puerto Rico in the spring of 1797. This sample would therefore be 225 years old, and is one of the oldest specimens successfully analyzed by genome skimming to date. We constructed the sequencing libraries using 10 to 200 ng of double stranded DNA with TruSeq Nano HT Sample kit (Illumina), following the default instructions. Each sample was paired-end sequenced (150 bp) on an Illumina HiSeq3000 lane and multiplexed with samples from different projects, and shotgun sequenced through the facilities of the Genopole platform of Toulouse. Finally, to assemble the plastid genome and the nrDNA cluster, we generated a consensus sequence for each region for each accession, and mapped reads onto them to check assembly quality in GENEIOUS v9.0.5 (https://www.geneious.com). We then annotated the plastid genomes using GeSeq (Tillich *et al.*, 2017) by choosing genomes of other species in the same genus available in GenBank as reference.

PHYLOGENETIC INFERENCE

For our tree search approach, we estimated a maximum likelihood (ML) phylogenetic tree for the MMP clade along with outgroups within Oleaceae, and outside of the family (Supplementary Table S1). We used a concatenated matrix of 19 regions that included 15 plastid regions (genes *matK*, *rbcL*, *rpoC2*, *rps16*, *trnK*, *ycf1*, *ycf2*, and intergenic spacers *atpB-rbcL*, *psbA-trnH*, *psbJ-*

petA, *rpl32-trnL*, *trnL-trnF*, *trnQ-rps16*, *trnS-trnG*, *trnT-trnL*), the nrDNA cluster, the two copies of *phy*B (*phy*BI and *phy*BII), and *phy*E. With such a selection of partitions, we maximized the number of partitions shared between the different accessions, included some highly informative plastid genes (Walker *et al.*, 2019), and had shorter computational times for further analyses. We used the program IQ-Tree v2.0.6 (Minh *et al.*, 2020) to estimate a species tree and assess the genealogical concordance between partitions. Specifically, we first did ten rounds of substitution model and partition scheme selection using ModelFinder (Kalyaanamoorthy *et al.*, 2017). With the best partition scheme and the best-fit model per partition at hand (the one with the lowest BIC score), we estimated a species tree using a concatenation approach with an edge-linked proportional partition model (Chernomor, Von Haeseler & Minh, 2016) and assessed branch support with 1000 ultrafast bootstrap replicates (Hoang *et al.*, 2018). The use of an edge-linked partition model for our concatenated multi-gene alignment allows for each of our partitions to have its own substitution model and evolutionary rate. Finally, we quantified the concordance between all partitions by calculating the gene concordance factor (gCF) and the site concordance factor (sCF) for each branch of the phylogenetic tree (Minh, Hahn & Lanfear, 2020). The gCF represents the fraction of gene trees that is concordant with a given branch, and the sCF shows the proportion of alignment sites that support that branch.

TREE TIME CALIBRATION

We further complemented our species tree inference with time calibration. We dated our best ML tree using a penalized likelihood approach in treePL (Smith & O'Meara, 2012). To generate confidence intervals for the node ages, we made 500 bootstrap trees (i.e., trees with the same topology as the best ML tree but with varying branch lengths) and dated them as well (Magallón *et al.*, 2015; Lagomarsino *et al.*, 2016). We determined the best value for the smoothing parameter by cross-validation, where we tested 21 smoothing values, separated by one order of magnitude (from 1e-15 to 1e+6), using the best ML tree as input. To calibrate our trees in treePL, we used one fossil calibration point for the root node. We used the *Fraxinus* L. fossil described by Call & Dilcher (1992) to set the minimum and maximum age of the stem age of the *Fraxinus* lineage. Samaras of *Fraxinus wilcoxiana* Berry, an extinct lineage, are from Middle Eocene sediments in two different locations in the USA (Call & Dilcher, 1992). We then set the minimum and maximum ages of the root node as the boundaries of the Middle Eocene stage, 37.8 and 47.8 Mya, respectively. We finally summarized the age statistics of internal nodes from the 500 bootstrap trees with TreeAnnotator v1.7.5 (Drummond et al., 2006), using the best ML tree, dated, as the input target tree.

HISTORICAL BIOGEOGRAPHY ESTIMATION

We used the R package "BioGeoBEARS" v1.1.2 (Matzke, 2013, 2014, 2018) to estimate ancestral ranges in the MMP+Eurasian *Osmanthus* clade. We tested six different methods: DEC (Dispersal–Extinction–Cladogenesis; Ree & Smith, 2008), DIVALIKE and BAYAREALIKE, and their variation with the addition of the jump dispersal parameter (*j*). All methods include parameters for anagenetic processes of dispersal and extinction, and for the cladogenetic event of sympatry when a single, widespread range is considered. They further diverge on what other cladogenetic processes are considered, the main difference being what type of vicariance events are allowed: DIVALIKE includes two possibilities for vicariance events, DEC only allows one type, and BAYAREALIKE excludes the possibility of vicariance completely (phylo.wikidot.com/biogeobears). Beyond the default approaches, the final parameter that was

turned on and off for each of those methods was *j*, which is equivalent to range switching at a node, leaving one daughter lineage in a new range and the other daughter lineage retaining the ancestral one (Matzke, 2014). Given the issues with direct statistical comparison between biogeographic models (Ree & Sanmartín, 2018), we implemented all methods in parallel, and used Akaike weights (Burnham & Anderson, 2002) to rank the fit of each model to the data. We estimated all models using as input the best ML tree found in our tree search.

For these biogeographic analyses, we classified native species distributions into four areas: (A) area comprising Macaronesia, the Mediterranean Region, and the Caucasus, (B) eastern Asia, (C) Australia, New Caledonia, and New Zealand, and (D) Hawaiian Islands. We classified species distributions based on the distribution data presented in Plants of the World Online (POWO, 2021). In addition, we used a matrix of manual dispersers (with the exponent parameter *w* turned on) that represented the probabilities of dispersals between the areas as a qualitative assessment of the distance between the areas.

RESULTS

CONGRUENCE BETWEEN DATASETS

Our final matrix had 64 accessions with seven partitions and 48,970 total sites (with ca. 21% of missing data), where 2,497 sites were parsimony-informative (ca. 5%). The original 19 partitions were rearranged in a new, 7-partition scheme (Table 3) following the selection of models of substitutions. Most of the data came from plastid partitions, where the number of sequences per partition ranged from 51 to 64. For partitions of nuclear DNA, we used 49 sequences for nrDNA, and 29 sequences for all phytochromes (Table 3).

We found that high bootstrap support values are coupled with moderate to low values for gene and site concordance factors. The variation at both the concordance at “gene” and site levels is a result of a dataset with an unbalanced number of sequences per accessions, and low number of parsimony-informative sites. Only ca. 45% of our accessions had sequences for all 19, original partitions, with some accessions having only one or two regions sequenced, notably the ones within *Notelaea*.

Here, we report and comment on the results for the major clades in our tree, i.e., clades with deeper ancestral nodes in the tree (Fig. 1). Most major clades have more than 75% bootstrap support, with one exception: the subclade that shows *Phillyrea* as sister to the *Nestegis*, *Notelaea* and 'Notosmanthus' group. The results showed that *Phillyrea* and *Picconia* are more closely related to *Nestegis*, *Notelaea* and 'Notosmanthus', than they are to the species in Eurasian *Osmanthus*. But the placement of *Phillyrea*, and by consequence the placement of *Picconia*, was not clear with this dataset. This uncertainty would be translated into three potential scenarios for their placement; a first one (the one reported here) with *Picconia* as sister to the rest of MMP, a second one where *Phillyrea* is instead the one sister to all other MMP species, and a third scenario where *Picconia* and *Phillyrea* are sister and this clade is in turn sister to the remaining species in MMP.

PHYLOGENETIC RELATIONSHIPS

Our best ML tree shows that MMP taxa are monophyletic and sister to Eurasian *Osmanthus*, within which the Caucasian *O. decorus* is sister to the eastern Asian species (Fig. 1). Within the MMP clade, the Macaronesian *Picconia* is shown as sister to a clade formed by *Phillyrea* and the remaining MMP taxa, although the placement of *Picconia* and that of *Phillyrea*, is not well supported. Furthermore, *Nestegis sandwicensis* (A.Gray) O.Deg., I.Deg. & L.A.S.Johnson, native to the Hawaiian Islands, is sister to the South Pacific subclade formed by the remaining four species in *Nestegis*, the nine *Notelaea* species, and all species in 'Notosmanthus'. Within this subclade, *Notelaea* is monophyletic, the four species of *Nestegis* also cluster together, and the same goes for 'Notosmanthus' taxa (Fig. 1). All the subclades show a clear geographic signal, each being restricted to a particular area: Australia, Hawaiian Islands, Macaronesia, Mediterranean Region, New Caledonia, and New Zealand.

This is the first time that most currently accepted 'Notosmanthus' taxa are included in a phylogenetic analysis. While these taxa are phylogenetically distinct from their Eurasian counterparts (Fig. 1), leaving no doubt about the need to dissociate taxonomically these two groups, relationships within 'Notosmanthus' are rather unclear. Three accessions of *O. austrocaledonicus* (subsp. *collinus* P.S.Green and subsp. *badula* P.S.Green) form a clade, which is sister to *O. cymosus* (Guillaumin) P.S.Green + *O. monticola* (Schltr.) Knobl. Another accession of *O. austrocaledonicus* subsp. *collinus* is sister to *O. austrocaledonicus* var. *crassifolius* Guillaumin, and the two are sister to all other New Caledonian *Osmanthus*.

The phylogenetic results highlight the taxonomic complexity of the Pacific taxa and provide the framework for a generic re-circumscription. As it is, the issue resides in the recognition of *Nestegis*, *Notelaea*, and 'Notosmanthus' as distinct taxa, especially in the context of a paraphyletic *Nestegis* and a polyphyletic *Osmanthus* with regards to 'Notosmanthus'. While recognizing four genera is a possibility, for reasons laid out later on (see Discussion), we opt for a single genus to be called *Notelaea s.l.* (Fig. 1; nomenclatural changes are presented in Appendix 1). Thus recognized, *Notelaea s.l.* is sister to *Phillyrea*, and is an evolutionary lineage that diversified in the Pacific region. The new names recognized under *Notelaea s.l.* (Appendix 1) will be used in the biogeography sections of both the Results and Discussion for ease of presentation.

DIVERGENCE TIMES AND HISTORICAL BIOGEOGRAPHY

The analyses of divergence time estimation place the beginning of the diversification of the MMP clade in the Early Miocene (at ca. 23 Mya), and the divergence between the major subclades within it during the Early-Middle Miocene (up to ca. 15 Mya; Fig. 2). Our estimates for node ages show a large interval for many nodes because of the single calibration point at the root of the tree. Even though intervals are broad, the median age estimates are consistently closer to the lower age limit than it is to the upper one (Table 4). Further, the node ages on our ML tree (and so on the tree used for our biogeographic analyses), are close to the median estimates but tend to be slightly older (Table 4).

The best-fit biogeographic model was the DEC+*j* (Table S1). With this model, the best prediction for the ancestral range of the whole clade was a range that combines areas A and B, which includes the Mediterranean Region, Macaronesia, and Asia. The probability of this range

is high (ca. 95%). That range is also estimated as the ancestral one for the Eurasian *Osmanthus* (94% probability). Within Eurasian *Osmanthus*, this ancestral range is split between *O. decorus* that is native to the Caucasus region, and the remaining species that show a range reduction towards an Asia-only distribution (Fig. 2). The ancestral range of the MMP clade is area A, with a high probability of 98%. This ancestal range would likely be estimated under any of the scenarios for the placement of *Picconia* and *Phillyrea*, mainly because of the lack of overlap between the range of these two genera and the ranges of the other species in the group. Further, we found a similar result for the ancestral range of the clade formed by *Phillyrea*+*Notelaea s.l.* (94% probability of being range A), and for the ancestral range of both *Picconia* and *Phillyrea* (ca. 99% in both cases), with species in *Picconia* later restricting their range to Macaronesia, and the ones in *Phillyrea* to the Mediterranean Region and the Canary Islands. Finally, the ancestor of *Notelaea s.l.* is estimated as area D, or the Hawaiian Islands (94% probability). *Nestegis sandwicensis* then keeps this ancestral range, but the ancestor of the remaining of *Notelaea s.l.* species shifts its range to area C, and each main lineage within this clade has geographically isolated itself from the other taxa among the three sub-areas that form area C (Fig. 2).

DISCUSSION

PHYLOGENETIC RELATIONSHIPS AND TAXONOMIC IMPLICATIONS

This study provides the framework for addressing the taxonomy of the MMP clade to stabilize the classification of this part of Oleaceae. Indeed, this molecular phylogenetic framework (Fig. 1), based on an extensive sampling of this group, presents us with a new way to delimit the generic complex long identified by Green (1958, 1963a; see also Baas *et al*., 1988; Wallander & Albert, 2000; Wallander, 2001), specifically comprised of *Nestegis*, *Notelaea*, 'Notosmanthus' (rather than Eurasian *Osmanthus*), *Phillyrea*, and *Picconia*. The results show six subclades within the MMP clade, which are each endemic to their particular region but are morphologically quite similar (Table 2).

Morphology in light of the molecular framework

These results highlight the challenges with morphology-based taxonomy wherein groups may be defined based on plesiomorphic or homoplastic characters. The broad morphological overlap seen in the MMP clade (likely a result of retention of ancestral morphology through diversification) aggravates such challenges. The New Caledonian species had, for instance, mostly been described within *Notelaea*. But Johnson (1957) united them within *Gymnelaea*, with the species from New Zealand and Hawaiian Islands as well as one Australian species (*Notelaea ligustrina* Vent.), based on aestivation and inflorescence types, and presence of microcrystalline deposits. He later transferred the species he recognized under *Gymnelaea* to *Nestegis*, which has priority (Johnson, 1958). Green (1963a,b, 1968), for his part, took a cautious approach of broadly-defined genera in anticipation of more discovery worldwide that would drastically alter the taxonomy of this and any other clade within the family. Yet, within the last five decades, only three new species were added to the MMP clade; all within *Notelaea* [namely *N. ipsviciensis* W.K. Harris (2004), *N. lloydii* Guymer (1987), and *N. pungens* Guymer (1987)] and none came from outside the known geographic range of the clade or improved our broad understanding of morphological variations within it. Other additions in *Osmanthus* clustered

within its Eurasian clade and, in the context of the current molecular sampling and taxonomy, no member of non-MMP genera fell within this clade. Thus, the lack of distinct morphological boundaries, the clear geographic patterns, and the absence of interference from taxonomic novelties that may otherwise induce different interpretations of relationships strengthen our conviction that our proposed generic re-circumscription within this clade would offer a robust and stable classification.

New classification of the MMP clade

Here, we use broad geographic distributions as our main guiding character to reorganize the six subclades within MMP. We kept the Macaronesian and Mediterranean species of *Picconia* and *Phillyrea*, respectively, as separate clades as they are currently recognized. In this study, they are shown as belonging to the MMP clade but their position is not well resolved. In fact, in a preliminary analysis with a reduced molecular dataset, *Picconia* and *Phillyrea* were shown as sister to each other, but also with low support. Given this uncertainty, but the clear geographical pattern, we decided it was best to consider those genera as currently distinct until further evidence. For the remaining four subclades, now in areas in the Pacific, the results (Fig. 1) present us with the option of recognizing either four genera, corresponding to each area: i.e., the Hawaiian Islands (an undescribed monotypic genus to accommodate *Nestegis sandwicensis*), Australia (*Notelaea s.s.*), New Caledonia (*Osmanthus* section *Notosmanthus* raised to generic rank), and New Zealand (*Nestegis s.s.*), or a single broadly defined genus. It can be argued that some lineages do present unique morphological characters. For instance, *Nestegis sandwicensis* can be distinguished from New Zealand *Nestegis* (Table 2) by the presence of a corolla, consistently four stamens, and hermaphroditic flowers only (vs. absence of corolla, two or four stamens, and hermaphroditic and male flowers). And, as previously discussed, 'Notosmanthus' can also be clearly distinguished from Eurasian *Osmanthus* (Table 2; Green, 1963a). However, even considering those examples, broad morphological overlap remains among the four subclades, and clear apomorphies are not readily identified. It seems that these taxa are not divergent enough in the context of the morphological characters thus far considered (e.g., Table 2) to be readily distinguished as four genera. Therefore, we opt to recognize a single genus that accounts for the lack of morphological distinctiveness among these taxa, which is also reflected in the extensive and frequent synonymies exercised within the MMP clade (Johnson 1957, 1958; Green 1958, 1963a,b, 1968). Thus, we are here recognizing the full Pacific group as the genus *Notelaea s.l.*, whose name has priority over the others (Table 1; Turland *et al.*, 2019). As broadly circumscribed, *Notelaea* comprises 21 species (including the five *Nestegis*, 12 *Notelaea*, and four *Osmanthus* section *Notosmanthus*) that are endemic to their particular areas (i.e., Australia, Hawaiian Islands, New Caledonia, and New Zealand). The last comprehensive species-level revision of members of *Notelaea s.l.* was completed by Green (1963a,b, 1968, 1998). All nomenclatural changes are presented in Appendix 1.

Remaining taxonomic implications in the MMP-Eurasian Osmanthus group

Beyond the elucidation of the generic limits within the MMP clade, we bring to light the need for the revision of some infrageneric taxonomy in the MMP-Eurasian *Osmanthus* group. For instance, the classification of the subspecies and variety in *O. austrocaledonicus* are not unequivocal. *Osmanthus austrocaledonicus* var. *crassifolius* is shown as distantly related to three of the other accessions of *O. austrocaledonicus* (subspp. *badula* and *collinus*), which form a monophyletic group. This morphologically distinct taxon restricted to high elevation scrub on

ultramafic rocks of Mount Humboldt and Mount Kouakoué is probably better treated at the species rank as it was originally described, and that is what we present in the nomenclatural appendix. One accession of *O. austrocaledonicus* subsp. *collinus* (*Munzinger et al. 823*) is nevertheless problematic as it falls near var. *crassifolius* instead of the clade formed by the subspp. *collinus* and *badula*. Because this sample was collected on Mont Nakada, not very far away from Mount Kouakoué where the accession of var. *crassifolius* was collected, we suspect a possible chloroplast capture. An ancient hybridization event between these species could explain the transfer of genetic markers from one species to another and therefore their apparent paraphyly. Population genetic analyses would be the next step to clarify species limits in this complex (e.g., Manawaduge, 2021).

As another example, our results incidentally show that Green's sectional classification within the genus *Osmanthus* (1958, 1963a) does not hold up in light of phylogenetic inferences. Beyond *Osmanthus* section *Leiola* (Spach) P.S.Green having recently been split and recognized as the new genus *Chengiodendron* C.B.Shang, X.R.Wang, Yi F.Duan & Yong F.Li (Li *et al.*, 2020) on one hand, and the resurrected genus *Cartrema* Raf. (Nesom, 2012) on the other hand, we find that *Osmanthus* section *Linocerioides* P.S.Green (incl. *O. didymopetalus* P.S.Green) and *O.* section *Siphonosmanthus* Franch. (incl. *O. delavayi* Franch. and *O. suavis* King ex C.B.Clarke) are not natural groupings. Both sections *Linocerioides* and *Siphonosmanthus* are embedded within *O.* section *Osmanthus* to which *O. decorus* and all other species belong (Fig. 1). Consequently, it would no longer be relevant to recognize the sections as none of them is monophyletic except for those that are distant from Eurasian *Osmanthus* (i.e., the former *O.* section *Leiola* and *O.* section *Notosmanthus*). Those two examples reinforce the complexity of the taxonomy within the clade studied here, and in the family as a whole as synonymization has been frequent among its genera. The path forward is to do more infrageneric phylogenetic studies to unravel the intricate patterns within this economically important family.

DIVERGENCE TIMES

Our estimates of divergence times of the MMP clade place the beginning of its diversification at Early Miocene, at ca. 23 Mya. The age estimates we present are older than those from other published works. For instance, Olofsson *et al*. (2019) reported a crown age for MMP as 15.99 Myr (with a range of ca. 20-13 Myr). Li *et al*. (2019), with a smaller Oleaceae sample as part of their dataset representing most angiosperms clades, estimated that the split between *Olea* and *Fraxinus* took place between 15.6 and 9.5 Mya, which would likely place the crown node of MMP at an even younger age. Smith & Brown (2018) show in their megaphylogenetic tree, based on all available GenBank data, a mean crown age for MMP as 10.5 Myr. We attribute the difference in our results and the mentioned studies to the difference in input sequence data, and molecular dating approaches. In the case of the studies by Olofsson *et al*. and Li *et al*. their datasets were composed only of plastid sequences. In the case of Smith & Brown's work, their data were likely driven by plastid sequences too with some species with nrDNA data. Those contrast with our dataset of both plastid and nuclear regions, the latter not being restricted to the nuclear ribosomal complex. Additionally, the choice of fossils and secondary calibration points can have important effects on the final node ages (Sauquet *et al.*, 2012). The approaches used here differ from those of the aforementioned studies as we only added one age constraint to the root of the phylogenetic tree, based on a *Fraxinus* fossil from an extinct species dated from the Middle Eocene (37.8-47.8 Mya; Call & Dilcher, 1992). In fact, the use of other fossils in our

preliminary analyses [fossils from other *Fraxinus* lineages (Palamarev, 1989; Jung & Lee, 2009)] produced age estimates that would consistently show only the minimum constraint ages as the best estimates. This likely shows that any analysis with information from *Fraxinus* fossils needs a more extensive sampling of this genus, instead of just having some representative lineages. Indeed, the age estimates presented here, or those for any group with a reduced fossil record, should be taken with caution.

BIOGEOGRAPHIC IMPLICATIONS

Our biogeographic results show that the ancestor of the MMP+Eurasian *Osmanthus* clade had populations spread out in different parts of Eurasia. Within the Eurasian *Osmanthus*, the Caucasian *O. decorus* is isolated from the remaining species that are all found in eastern Asia. Green (1972) pointed out this same disjunct, Asiatic-European distribution within *Osmanthus*, and added that other Oleaceae genera (*Fontanesia* Labill., *Forsythia* Vahl, *Ligustrum* L., and *Syringa* L.) present a similar pattern. Outside of Oleaceae, taxa in likely eight other plant families also have such a distribution, although the pattern of many species in Asia and few species in Europe can be opposite in some cases (Browicz, 1992). The causes of such a disjunct Asiatic-European distribution are speculative but the two main ones are likely the uplift of the Qinghai-Tibetan Plateau (QTP) and cooling of global temperatures during the Miocene. The rapid uplift of the QTP in the Early Miocene (ca. 23 to 16 Mya), associated with lower temperatures, created physical and climatic barriers for the dispersals between Europe and eastern Asia (Harrison *et al.*, 1992; Zachos *et al.*, 2001). Another consequence was the aridification of Central Asia due to the changes in the precipitation patterns in the region (Miao *et al.*, 2012), which in turn could have caused local populations to go extinct and contribute to vicariance events between Europe and Asia.

In the MMP clade, within the regions of what we called area A (Macaronesia, Mediterranean, Caucasus), the likely range evolution from East to West is compatible with islands' ages. At the earliest, although unlikely case, the Macaronesia region could have been reached at ca. 23 Mya (age of the root node). This would place the diversification of taxa in that area at the beginning of the formation of current islands in the Macaronesia archipelagos (Hoernle & Carracedo, 2009; Fernandez-Palacios *et al*., 2011; van den Bogaard, 2013; Ramalho *et al.*, 2015), where the oldest island in the archipelagos considered for this study (Fuerteventura, on the Canary Islands) formed ca. 23 Mya (Hoernle & Carracedo, 2009; van den Bogaard, 2013); knowing that other islands in the region, which are now fully submerged, formed as early as 60 Mya (Férnandez-Palacios *et al*., 2011). A more plausible explanation would be that the colonization of Macaronesia by MMP species happened at later times, potentially as late as the Pleistocene (ca. 3 Mya), as it is the case for other plant species that are today native to the islands (e.g., Navarro-Pérez *et al*., 2015; Jaén-Molina *et al*., 2021).

Placing the early diversification of the remaining of the MMP clade, especially on how it reached the Pacific region, remains an open question though. In this analysis, an ancestor distributed in the Macaronesian/Mediterranean Region reached the Pacific having the Hawaiian Islands as its point of entrance (Fig. 2), between ca. 22 and 10 Mya (considering age range intervals from Table 4). These dates agree with data on geological dynamics of the islands in the Hawaiian archipelago that show that small islands, now submerged, started forming in the vicinity as early as 32 Mya (Price & Clague, 2002). Now, there are two possibilities for the route of this range evolution. The first hypothesis is that the directionality of the range expansions

could have been from East to West. After the clade expanded throughout the Mediterranean and Macaronesian regions, it could have reached the Pacific region either by the means of sea currents through the still open Central American seaway (see both Montes *et al.*, 2012, and O'Dea *et al.*, 2016) that allowed westward currents to flow from Africa directly into the central Pacific, or by the use of birds as dispersers. The second hypothesis would be of a West-East direction of range evolution, where parts of Asia are recolonized all the way to East Asia, with further island-hopping down the Hawaiian chain of islands, also with the help of birds as dispersal vectors. While we do not have enough data to support one hypothesis over the other, analyses on the origins of the Hawaiian flora have shown that ca. 4% of the endemic species in the islands likely have an East Asian origin (where most of the native species have an Indo-Malayan and/or Pacific islands origin; Fosberg, 1948; Price & Wagner, 2018); two examples with such a migration route are the monotypic genus *Hillebrandia* (Begoniaceae), endemic to the Hawaiian Islands (Clement *et al*., 2004), and *Hesperomannia* (Asteraceae; Kim *et al*., 1998).

Independent of how the Pacific region was reached, the distribution of the MMP taxa within the Pacific region is a consequence of dispersals between those areas, and not continental vicariance (especially between Australia, New Caledonia and New Zealand). The Zealandia/Te Riu-a-Māui continent, that includes the islands of New Zealand and New Caledonia, has a complex geological history with a long period of submersion (partial or total) during the Late Cretaceous and Early Paleogene (Neall & Trewick, 2008). It is suggested, though, that the final emersion of New Caledonia started between 34 and 25 Mya, with continuous emergence since 25 Mya (Pillon *et al*., 2021). Our estimates of dispersals to New Caledonia between 17.7 and 10.2 Mya (node and stem age for the clade of *Notelaea austrocaledonica* Vieill. + *N. monticola* Guillaumin + *N. cymosa* Schltr.) are consistent with this scenario. In the case of New Zealand, there is a lot of debate about the existence of a period of full immersion up to ca. 25-23 Mya (Landis *et al*., 2008; McCulloch & Waters, 2019), or only partial (Wallis & Jorge, 2018), since the separation of Australia and Zealandia/Te Riu-a-Māui in the Upper Cretaceous (ca. 85 Mya; Bache *et al.*, 2014). Nevertheless, even with a full immersion period, the diversification of *Notelaea* species in New Zealand starting at ca. 17 Mya does not conflict with the islands' ages. These divergence ages add support to the argument that the flora (and fauna) of New Caledonia and New Zealand is formed mostly/exclusively by lineages that arrived through long-distance dispersals (Pole, 1994), and not by lineages that pre-date the breakup of the Gondwana continent.

The disjunct nature of the distribution in the small, MMP+Eurasian *Osmanthus* clade might indicate that these are relict taxa. For instance, *Picconia* species might be examples of taxonomic palaeoendemic lineages. This is a hypothesis presented by Cronk (1992) that lists Macaronesian species of different families that are endemic or of isolated position in a clade with disjunct distribution, that diversified during the Miocene, and whose closest relatives were species with African distribution that are now extinct (Cronk, 1992, 1997). The lack of fossil data makes it hard to fully support that hypothesis, although such an explanation could be the reason why the placement of *Picconia* in the phylogenetic tree is still uncertain. This pattern of extant species that are remnants of ancient, more widespread African flora is also reported by Sanmartín *et al.* (2010). Further, Oceania (East Australia, New Caledonia) is known to harbor many relictual angiosperm families, likely as a result of having great climatic stability since the Late Cretaceous (Morley, 2001). Such stability was possibly a factor that guaranteed the persistence of lineages of the MMP clade in the region, contrasting with other regions that suffered environmental changes due to the climatic fluctuations during the Miocene. Even

though we can only speculate on the actual causes of the distribution of the MMP+Eurasian *Osmanthus* clade, the highly disjunct distribution of this small clade seems to point to local extinction as a major player in the evolution of its distribution.

Beyond its wide geographic distribution, the MMP clade displays a wide range of ecological preferences. Its members occur within climate regimes that range from cool temperate (Tasmania and the South Island of New Zealand) to warm tropical (Hawaiian Islands, including monsoon in northern Australia) and Mediterranean. They also grow on diverse substrates that range from volcanic in Macaronesia, Hawaiian Islands, and Norfolk, to ultramafic in New Caledonia. Similarly, there is a great diversity of sexual system in this small group (Table 2), ranging from hermaphroditism in *Nestegis sandwicensis* (Sakai *et al.*, 1995), *Notelaea* (Green, 1968, 2004), and *Picconia* (Green, 2004) to androdioecy in 'Notosmanthus' (and in *Osmanthus s.s.* for that matter; Green, 1958, 1963a, 1998), *Phillyrea* (Lepart & Dommée, 1992; Green, 2004), and possibly in *Picconia* as well (Artega *et al.*, 2006; Ferreira *et al.*, 2011), and even polygamy in New Zealand *Nestegis* (Green, 1963b; Wagner, Herbst & Sohmer, 1999). Such variability in sexual reproduction is considered a hallmark of lineage diversification and facilitates adaptive radiation (Barrett, 2013). Indeed, with presumed good dispersal capability and climatic adaptation as well as a reproductive versatility conducive to adaptive radiation, it is rather remarkable that this group is not more speciose nor more widely distributed.

CONCLUSIONS

With phylogenomic data and an extensive sampling, this study allowed us to address the long-standing problematic generic circumscription within the MMP clade. While the phylogenetic placement of *Phillyrea* and *Picconia* remains unclear, the remaining Pacific taxa are herein considered as members of *Notelaea s.l.* This latter genus, now comprised of 21 species, occurs in Australia, Hawaiian Islands, New Caledonia, New Zealand, and Norfolk Island. In a larger context, this study brings about a much needed order within at least a part of Oleaceae, with the hope that this updated generic circumscription stabilizes the classification for a long term. And while this study added some pieces to the puzzle, more infrageneric assessments are needed not only to improve current understanding of both relationships and morphologies within the family, especially within the polyphyletic *Chionanthus* (Besnard *et al.*, 2009; Hong-Wa & Besnard, 2013; Olofsson *et al.*, 2019; Dupin *et al.*, 2020), the paraphyletic *Jasminum* L. (Wallander & Albert, 2000; Lee *et al.*, 2007; Jeyarani *et al.*, 2018) and *Syringa* (Li *et al.*, 2002; Li *et al.*, 2012; Dupin *et al.*, 2020), but also to update the infrafamilial classification.

APPENDIX 1

Notelaea s.l. as herein circumscribed includes all species formerly recognized within *Nestegis*, *Notelaea s.s.*, and *Osmanthus* section *Notosmanthus*. The following combinations are thus made to accommodate species of *Nestegis* and *Osmanthus* section *Notosmanthus* within *Notelaea s.l.* For New Caledonian taxa, only homotypic synonyms are provided and heterotypic synonyms can be found in Green (1998).

Notelaea Vent., Choix Pl. 25. 1804.

Type: *Notelaea longifolia* Vent.

≡ *Postuera* Raf., Sylva Tellur.: 10. 1838. Type: *Postuera longifolia* (Vent.) Raf.

= *Nestegis* Raf., Sylva Tellur.: 10. 1838. Type: *Nestegis elliptica* Raf. nom. illeg. ≡ *Olea apetala* Vahl, Symb. Bot. 3: 3. 1794. ≡ *Gymnelaea apetala* (Vahl) L.A.S.Johnson, Contr. New South Wales Natl. Herb. 2: 412. 1957. ≡ *Nestegis apetala* (Vahl) L.A.S.Johnson, Fl. Hawaiiensis 300. 1958.

= *Osmanthus* section *Notosmanthus* P.S.Green, J. Arnold Arbor. 44: 269. 1963. Type: *Osmanthus austrocaledonicus* (Vieill.) Knobl. ≡ *Notelaea austrocaledonica* Vieill., Bull. Soc. Linn. Normandie 9: 345. 1865.

= *Rhysospermum* C.F.Gaertn., Suppl. Carp.: 232. 1807. Type: *Rhysospermum nervosum* C.F.Gaertn. ≡ *Notelaea nervosa* (C.F.Gaertn.) Steud., Nomencl. Bot. ed. 2, 2: 198. 1841.

Notelaea apetala (Vahl) Hong-Wa & Besnard, **comb. nov.**

Basionym: *Olea apetala* Vahl, Symb. Bot. 3: 3. 1794. ≡ *Gymnelaea apetala* (Vahl) L.A.S.Johnson, Contr. New South Wales Natl. Herb. 2: 412. 1957. ≡ *Nestegis apetala* (Vahl) L.A.S.Johnson, Fl. Hawaiiensis 300. 1958. Holotype: New Zealand, without locality, *ex Herb Vahl* (Nova Zelandia, 1773, *J.R. Forster s.n.*, [C10016095! image]).

= *Olea endlicheri* F. Muell., Fragm. (Mueller) 8: 43. 1872. **Lectotype (designated here):** Norfolk Island, without locality, *s.d., Ferd. Bauer s.n.* (W0046352! [image], isolecto-: W0046353! W0046354! [images]).

Distribution: New Zealand (North Island) and Norfolk Island.

Note: The specimen collected during the Bauer brothers' expedition was the only one known from Norfolk Island at the time it was described as *Olea endlicheri* by Mueller (1872). And although the species recognition based solely on geography was not justified, it was nonetheless validly published, and Bauer's specimen is thus chosen as the lectotype.

Notelaea austrocaledonica Vieill., Bull. Soc. Linn. Normandie 9: 345. 1865.

≡ *Osmanthus austrocaledonicus* (Vieill.) Knobl., Repert. Spec. Nov. Regni Veg. 41: 152. 1936. **Lectotype (designated here):** New Caledonia, Wagap, 1861-1867, *Vieillard 333* (P00096706!, remaining syntypes: P000967707!, P00096708!, P00096709!).

Distribution: New Caledonia.

Notelaea austrocaledonica var. ***badula*** (Vieill. ex Pancher & Sébert) Pillon & J.Dupin, **comb. nov.** & **stat. nov.**

Basionym: *Notelaea badula* Vieill. ex Pancher & Sébert. Rev. Marit. Colon. 40: 570. 1874. ≡ *Gymnelaea badula* (Vieill. ex Pancher & Sébert) L.A.S.Johnson, Contr. New South Wales Natl. Herb. 2: 413. 1957. ≡ *Nestegis badula* (Vieill. ex Pancher & Sébert) L.A.S.Johnson, Fl. Hawaiiensis 300. 1958. ≡ *Osmanthus badula* (Vieill. ex Pancher & Sébert) Hutch. ex S.Moore, J. Linn. Soc., Bot. 45: 356. 1921. ≡ *Osmanthus austrocaledonicus* subsp. *badula* (Vieill. ex Pancher & Sébert) P.S.Green, in Fl. Nouv.-Caléd. 22: 40. 1998. **Lectotype (designated here):** New Caledonia, *Pancher* (*Vieillard 2861*) (P00096812! [central top fragment]).

Distribution: New Caledonia.

Notelaea austrocaledonica var. ***collina*** (Schltr.) Pillon & J.Dupin, **comb. nov.** & **stat. nov.**

Basionym: *Notelaea collina* Schltr. Bot. Jahrb. Syst. 39: 229 (1906). ≡ *Gymnelaea collina* (Schltr.) L.A.S.Johnson, Contr. New South Wales Natl. Herb. 2: 413. 1957. ≡ *Nestegis collina* (Schltr.) L.A.S.Johnson, Fl. Hawaiiensis 300. 1958. ≡ *Osmanthus collinus* (Schltr.) Knobl., Repert. Spec. Nov. Regni Veg. 41: 152. 1936. ≡ *Osmanthus austrocaledonicus* subsp. *collinus* (Schltr.) P.S.Green, in Fl. Nouv.-Caléd. 22: 38. 1998. **Lectotype (designated here):** New Caledonia, Païta, 28 September 1902, *Schlechter 14834* (P00096862!)

Distribution: New Caledonia.

Notelaea crassifolia (Guillaumin) Pillon & J.Dupin, **comb. nov.**

Basionym: *Osmanthus crassifolius* Guillaumin. Mém. Mus. Natl. Hist. Nat. Sér. B, Bot. 4: 48. 1953. ≡ *Osmanthus austrocaledonicus* var. *crassifolius* (Guillaumin) P.S.Green, in Fl. Nouv.-Caléd. 22: 37. 1998. Type: New Caledonia, Mont Humboldt, 12 December 1940, *Virot 339* (holo: P00096752!, iso-: P00096753!)

Distribution: New Caledonia.

Notelaea cunninghamii (Hook.f.) Hong-Wa & Besnard, **comb. nov.**

Basionym: *Olea cunninghamii* Hook.f., Fl. Nov.-Zel. 1: 175. 1853. ≡ *Gymnelaea cunninghamii* (Hook.f.) L.A.S.Johnson, Contr. New South Wales Natl. Herb. 2: 412. 1957. ≡ *Nestegis cunninghamii* (Hook.f.) L.A.S.Johnson, Fl. Hawaiiensis 300. 1958. Lectotype: New Zealand, without locality, *s.d., Colenso s.n.* (K000978892! [image])

Distribution: New Zealand (North Island).

Notelaea cymosa Guillaumin. Bull. Soc. Bot. France 89: 232. 1942.

≡ *Osmanthus cymosus* (Guillaumin) P.S.Green, J. Arnold Arbor. 44: 270. 1963. Type: New Caledonia, Mont Mi, 9 March 1969, *Balansa 1222* (holo: P00076035!, iso-: P00101265!, P00076036!)

Distribution: New Caledonia.

Notelaea lanceolata (Hook.f.) Hong-Wa & Besnard, **comb. nov.**

Basionym: *Olea lanceolata* Hook.f., Fl. Nov.-Zel. 1: 176. 1853. ≡ *Gymnelaea lanceolata* (Hook.f.) L.A.S.Johnson, Contr. New South Wales Natl. Herb. 2: 412. 1957. ≡ *Nestegis lanceolata* (Hook.f.) L.A.S.Johnson, Fl. Hawaiiensis 300. 1958. Lectotype: New Zealand, without locality, *s.d., Colenso? Or Sinclair? s.n.* (K000978896! [image])

Distribution: New Zealand (North Island and South Island).

Notelaea montana (Hook.f.) Hong-Wa & Besnard, **comb. nov.**

Basionym: *Olea montana* Hook.f., Fl. Nov.-Zel. 1: 176. 1853. ≡ *Gymnelaea montana* (Hook.f.) L.A.S.Johnson, Contr. New South Wales Natl. Herb. 2: 413. 1957. ≡ *Nestegis montana* (Hook.f.) L.A.S.Johnson, Fl. Hawaiiensis 300. 1958. Lectotype: New Zealand, without locality, 1847, *Colenso 711* (K000978900! [image]).

Distribution: New Zealand (North Island and South Island).

Notelaea monticola Schltr. Bot. Jahrb. Syst. 39: 229. 1906.

≡ *Gymnelaea monticola* (Schltr.) L.A.S.Johnson, Contr. New South Wales Natl. Herb. 2: 413. 1957. ≡ *Nestegis monticola* (Schltr.) L.A.S.Johnson, Fl. Hawaiiensis 300. 1958. ≡ *Osmanthus monticola* (Schltr.) Knobl., Repert. Spec. Nov. Regni Veg. 41: 152. 1936. **Lectotype (designated here):** New Caledonia, Mont Humboldt, 16 November 1902, *Schlechter 15315* (P00096909!)

Distribution: New Caledonia.

Notelaea sandwicensis (A.Gray) Hong-Wa & Besnard, **comb. nov.**

Basionym: *Olea sandwicensis* A.Gray, Proc. Amer. Acad. Arts V: 331. 1862. ≡ *Gymnelaea sandwicensis* (A.Gray) L.A.S.Johnson, Contr. New South Wales Natl. Herb. 2: 414. 1957. ≡ *Nestegis sandwicensis* (A.Gray) O.Deg., I.Deg. & L.A.S.Johnson, Fl. Hawaiiensis 300. 1958. ≡ *Osmanthus sandwicensis* (A.Gray) Benth. & Hook.f. ex B.D.Jacks., Index Kew. 2: 380. 1894. **Lectotype (designated here):** Oahu, Sandwich Islands, U.S. South Pacific Expl. Exp., 1838-

1842, *Wilkes Explor. Exped. s.n.* (GH00075129! [image], isolecto-: NY00297305! US00435547! [images]).

Distribution: Hawaii.

Note: The specimen at US has the exact locality as provided in the protologue (i.e., "Oahu, Sandwich Islands"). However, it is very likely that it is the specimen at GH (with "Sandwich Islands" only), where Asa Gray was based, that he used for the species description and is therefore chosen as the lectotype. Other syntypes (Remy 479 [GH00075130!, P02983937!, US01154620! (images)] and Remy 482 [GH00075131!, P04861310! (images)]) are listed as mere additions as illustrated by the sentence "also in Remy's collection" (Gray, 1862).

DATA AVAILABILITY

The data and scripts underlying this article are available in Figshare, at https://dx.doi.org/[doi]

SUPPLEMENTARY MATERIAL

Table S1 - Information on accessions: species names, voucher information, geographic distribution, and data accession numbers.

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Table 1. Currently accepted genera of subtribe Oleinae, with year of description, number of species recognized, and distribution. Asterisks indicate members of the MMP clade.

Genus	Year described	Species recognized	Distribution
Cartrema	1838	4 (2[a])	Central and North America
Chengiodendron	2020	3 (5[a])	East Asia
Chionanthus	1753	ca. 150	America, Asia, and Oceania
Forestiera	1810	ca. 15	North and South America
Haenianthus	1864	3	Caribbean
Hesperelaea	1876	1 (extinct)	Guadalupe Island
*Nestegis**	1838	5	Hawaii, New Zealand, and Norfolk Island
Noronhia	1806	104	Africa and Madagascar
*Notelaea**	1804	12	Australia (including Tasmania)
Olea	1753	ca. 10	Africa, Madagascar, Mediterranean, Asia, and Oceania
Osmanthus	1790	28	East Asia and New Caledonia
[*O.* sect. *Notosmanthus*]*	[1963]	[3]	[New Caledonia]
*Phillyrea**	1753	2	Mediterranean (1 subsp in Macaronesia)
*Picconia**	1844	2	Macaronesia
Priogymnanthus	1994	4	South America
Tetrapilus	1790	23	Asia

a: two out of the four species of *Cartrema* currently recognized, *C. scortechinii* (King & Gamble) de Juana and *C. sumatrana* (P.S.Green) de Juana, most likely belong to the recently described genus *Chengiodendron*. Although the placement of *C. sumatrana* has not been assessed yet and that of *C. scortechinii* is not fully resolved (see Li *et al*., 2020), their morphology and geographic distribution would probably support a placement within *Chengiodendron*. The numbers we present in parentheses for *Cartrema* and *Chengiodendron* reflect this correction.

Table 2. A comparative table of selected features of the five genera within the MMP clade, with distinguishing characteristics of subordinate taxa of interest (in bold) put in brackets.

	Nestegis **[*N. sandwicensis*]**	*Notelaea*	*Osmanthus* **['Notosmanthus']**	*Phillyrea*	*Picconia*
Leaves	simple, entire	simple, entire	simple, entire/serrate **[entire]**	simple, entire/dentate	simple, entire/serrulate
Microcrystalline deposits	present/absent **[present]**	absent	absent	present	present
Breeding system	polygamodioecy **[hermaphroditism]**	hermaphroditism	androdioecy	androdioecy	hermaphroditism (and possibly androdioecy)
Inflorescences	racemose-decussate	racemose-decussate	umbellate-fasciculate **[racemose-decussate]**	racemose-decussate	racemose-decussate
Petals	absent **[present; connate; rotate]**	present; distinct; paired at base	present; connate; campanulate	present; connate; subrotate	present; distinct; paired at base
Aestivation	imbricate	induplicate-valvate	imbricate	imbricate	valvate
Stamens	2/4 (-3 or 6) **[4]**	2	2	2	2
Filaments	short **[obscure]**	short	short **[subsessile]**	short/subsessile	subsessile
Stigma	bifid **[bilobed]**	bilobed	capitate, slightly bilobed **[bilobed]**	capitate	capitate
Style	short **[subnull]**	subnull	short **[subnull]**	short	subnull
Ovary	conical	conical	rounded **[conical]**	conical	conical
Endocarp	hard	hard/crustaceous	crustaceous **[hard]**	crustaceous	hard
Chromosome number	2n = (44)-46[a] **[2n = 44(46)]**	2n = 46[b]	2n = 46[c]	2n = 46-(92)[d]	2n = 46[e]

Compiled from Endlicher (1838-1840), De Candolle (1844), Gray (1862), Vieillard (1865), Bentham & Hooker (1876), Knoblauch (1895), Johnson (1957, 1958) and Green (1958, 1963a,b, 1968, 1998, 2004), Guymer (1987), Lepart & Dommée (1992), Sakai *et al.* (1995), Wagner, Herbst, Sohmer (1999); Chromosome numbers from [a]Dawson (1995) and Kiehn (2005), [b]Green (1968) and Briggs (1970), [c]Taylor (1945), Briggs (1970) and Yang *et al.* (2018), [d]Taylor (1945), Cardona (1991) and Carré *et al.* (2021), and [e]Briggs (1970).

Breeding system: Some sexual systems can be fairly cryptic; not all species here have been studied in such detail.

Table 3. Best partition scheme and best-fit model per partition according to Bayesian information criterion (BIC) implemented in ModelFinder.

Partition	*Seq*	*Site*	*Unique*	*Infor*	*Invar*	*Const*	*Substitution Model*
atpB-rbcL spacer	56	846	111	43	783	783	K3Pu+F+R2
matK + *rpoC2* + *rps16* + *trnK*-partial + *trnL-trnF* spacer	64	8543	607	212	8079	8079	TVM+F+R3
ycf1 and spacers: *psbA-trnH* + *psbJ-petA* + *rpl32-trnL* + *trnQ-rps16* + *trnS-trnG* + *trnT-trnL*	60	12269	1595	678	10938	10938	TVM+F+R3
rbcL	54	1437	82	49	1367	1367	GTR+F+I+G4
ycf2	51	6870	106	33	6812	6812	K3Pu+F+I
nrDNA	49	8727	1363	873	7318	7318	GTR+F+I+G4
*phy*BI + *phy*BII + *phy*E	29	10278	5182	609	8433	8433	TN+F+R2

Seq: Number of sequences
Site: Total number of sites
Unique: Number of unique site patterns
Infor: Number of parsimony-informative sites
Invar: Number of invariant sites
Const: Number of constant sites (can be subset of invariant sites)

Table 4. Summary statistics of crown node ages for selected nodes from a sample of 500 bootstrap trees, and comparison with ages on ML tree shown in Fig 2.

MRCA	*Median*	*95% HPD (lower – upper)*	*Age ML tree*
Root node	19.5	23.8 – 14.7	23.2
Eurasian *Osmanthus*	9.4	11.8 – 6.8	12.8
Eurasian *Osmanthus* excluding *O. decorus*	7.0	8.6 – 5.3	9.5
MRCA of MMP clade	17.5	22.4 – 13.1	21.2
MRCA of *Phillyrea latifolia* and *N. apetala*	16.9	21.8 – 12.3	20.6
Picconia	6.6	9.5 – 4.1	8.4
Phillyrea	8.5	12.2 – 5.1	11.0
MRCA of *Notelaea s.l.*	15.3	20.7 – 10.5	18.9
MRCA of *Notelaea s.l.* excluding *N. sandwicensis*	14.1	19.0 – 9.1	17.7

MRCA: most recent common ancestor
Median: median age estimated from sample of 500 bootstrap trees
95% HPD: highest posterior density interval that contains 95% of the estimates for the node age
Age ML tree: node age on the ML tree in Fig. 1

Table S1. Biogeographic model selection in BioGeoBEARS. Best model in bold.

Model	*LnL*	*N params*	*d*	*e*	*j*	*w*	*AICc*	*AICc weight*
DEC	-19.00	3	6.0e-04	1.4e-03	0	-0.73	44.64	0.01
DEC+j	***-12.59***	***4***	***1.0e-12***	***1.0e-12***	***0.0004***	***-1.59***	***34.26***	***0.80***
DIVALIKE	-19.05	3	1.2e-03	1.0e-12	0	-0.52	44.74	0.01
DIVALIKE+*j*	-14.51	4	1.0e-12	1.0e-12	0.0054	-0.59	38.09	0.12
BAYAREALIKE	-28.84	3	1.8e-03	1.4e-02	0	-0.25	64.32	0.00
BAYAREALIKE+j	-14.97	4	1.0e-07	1.0e-07	0.0050	-0.63	39.02	0.07

LnL: log-Likelihood of the model
N params: number of free parameters estimated
d: rate of 'dispersal' (range expansion)
e: rate of 'extinction' (range contraction)
j: relative per-event weight of jump dispersal
w: exponent on manual dispersal multipliers (modifies *d*, *j*)
AICc: Akaike information criterion with a correction for small sample sizes
AICc weight: relative likelihood of the model divided by the sum of these values across all models

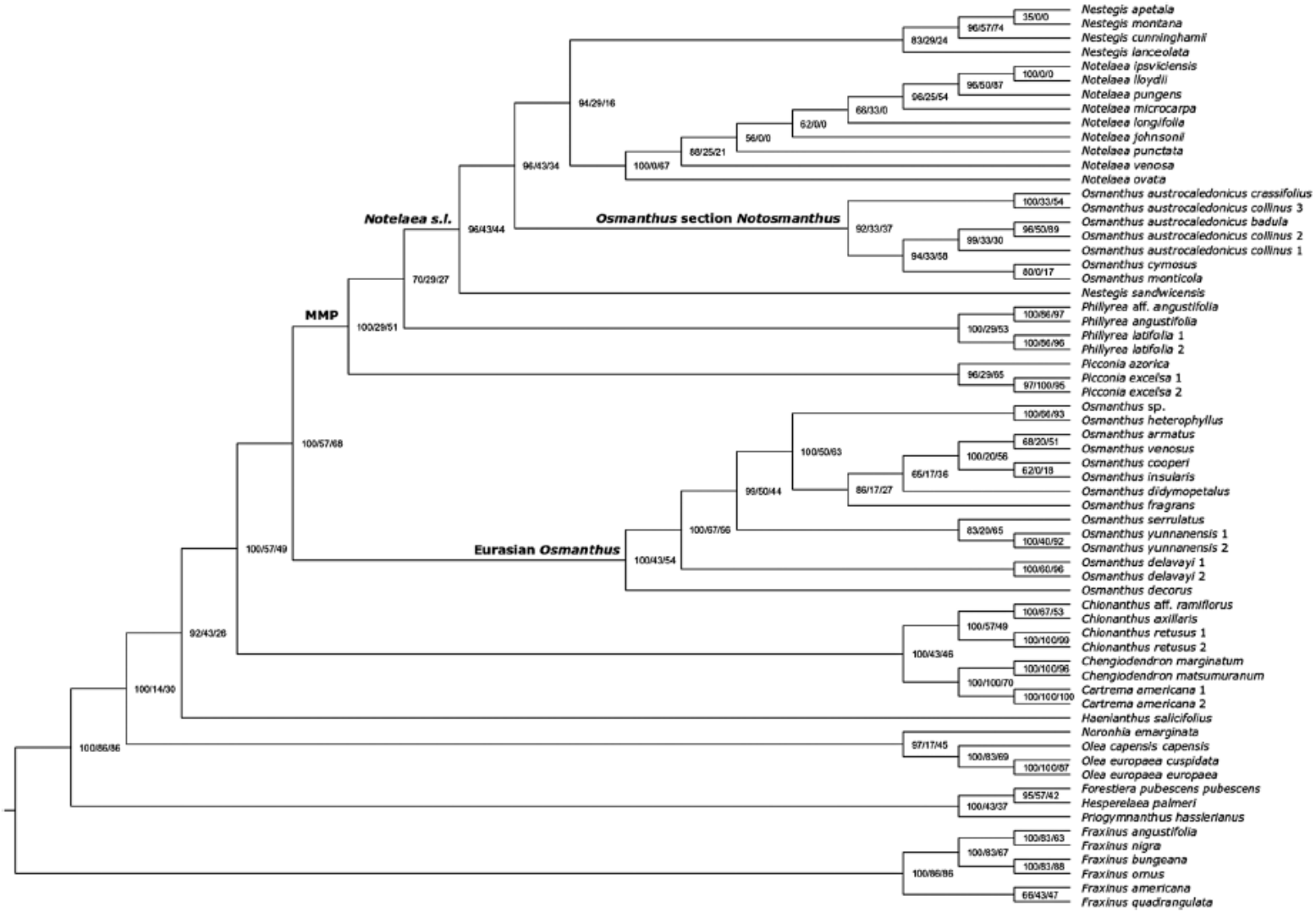


Figure 1. Cladogram based on the best ML tree found representing the relationships between the species in the MMP+Eurasian *Osmanthus* clade and outgroups, and the support for all clades. At each node, the three values represent: (1) the bootstrap support, (2) the gene concordance factor (gCF), and (3) the site concordance factor (sCF). Numbers at tip labels are explained in Table S1.

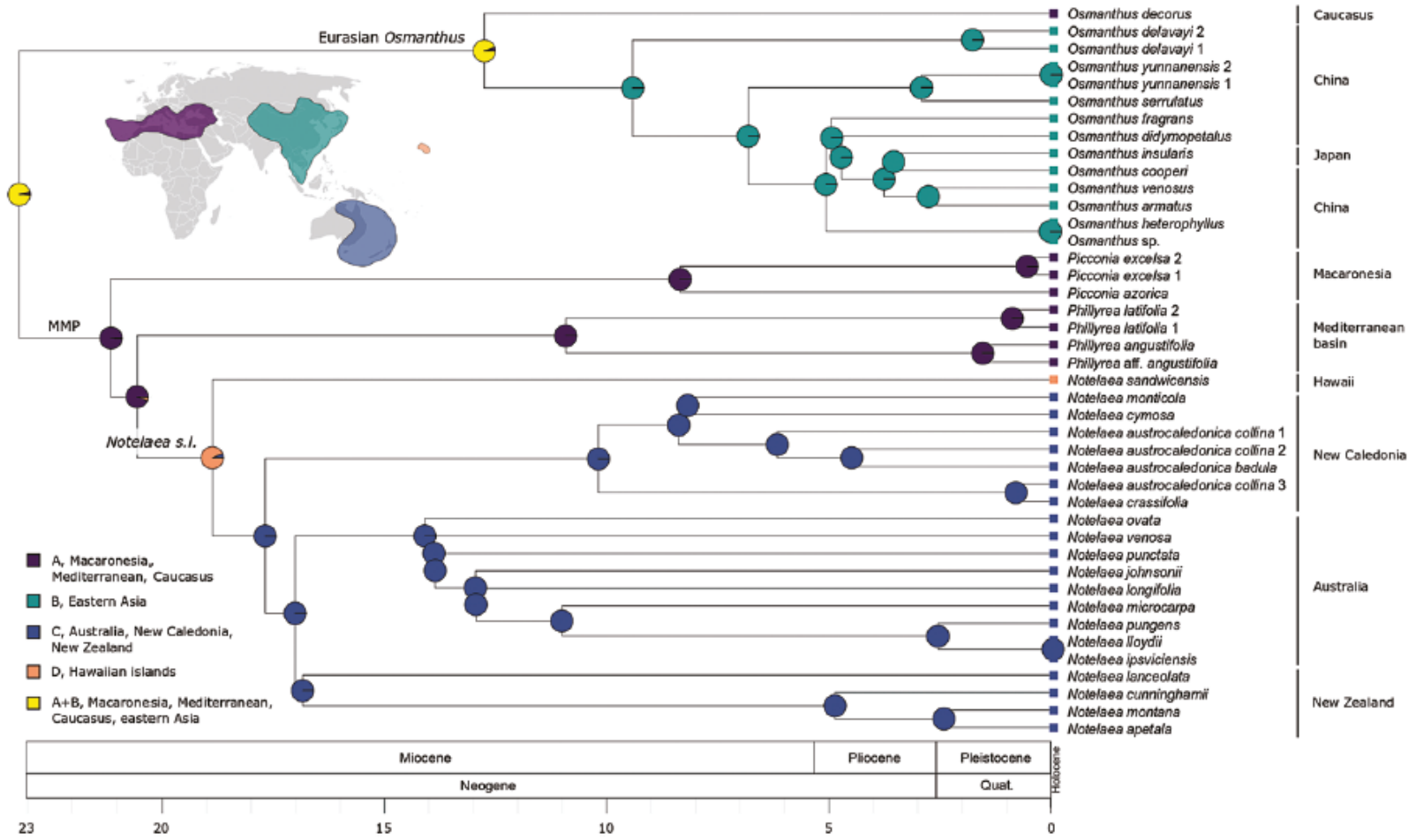


Figure 2. Summary of the biogeographic history of the MMP+Eurasian *Osmanthus* clade. The chronogram shown here is the dated, best ML tree from our tree search. At the tips, colored squares represent the distribution of each taxon, and at the nodes the pies show the estimated probability of ancestral ranges. Those node state probabilities result from the best biogeographic model for this data, DEC+*j*. Colors at the tips and nodes correspond to areas shown in the map, and are explained in the legend on the lower left. The locality of collection of each accession is shown to the right of the tip labels. Tip labels with numbers are explained in Table S1. The scale at the bottom represents time in millions of years from the present, and indicates the periods (bottom) and epochs (top).