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Towards a phylogenetic classification of the *Ocotea* complex (Lauraceae): classification principles and reinstatement of *Mespilodaphne*

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The large genus *Ocotea* (*c.* 400 species) has been known to be paraphyletic with respect to most other Neotropical genera of Lauraceae for almost 20 years, but a phylogenetic classification has not yet been proposed. Here we present a phylogenetic analysis, based on ITS and *psbA-trnH* sequences of 123 species from the *Ocotea* complex, focused on the Neotropical species with bisexual flowers. Our results show that several well-supported clades can be recognized morphologically. We discuss the principles of splitting monophyletic genera from large paraphyletic groups, and we reinstate the genus *Mespilodaphne* as a first step towards a phylogenetic classification. In addition, three species previously included in *Aiouea* are transferred to *Damburneya*.

ADDITIONAL KEYWORDS: classification principles – fruit morphology – internal transcribed spacer – *psbA-trnH* – paraphyletic groups – phylogenetic analysis – stamen morphology.

INTRODUCTION

Lauraceae include *c.* 50 genera with 2500–3500 species, mostly from tropical areas, with only a few in temperate regions (Rohwer, 1993a). The *Ocotea* Aubl. complex *sensu* Chanderbali, van der Werff & Renner (2001) consists of *c.* 700 species in 16 genera, *Aniba* Aubl., *Damburneya* Raf., *Dicypellium* Nees & Mart., *Endlicheria* Nees, *Gamanthera* van der Werff, *Kubitzkia* van der Werff, *Licaria* Aubl., *Nectandra* Rol. ex Rottb., *Ocotea* Aubl., *Paraia* Rohwer, H.G.Richt. & van der Werff, *Phyllostemonodaphne* Kosterm., *Pleurothyrium* Nees, *Povedadaphne* W.C.Burger, *Rhodostemonodaphne* Rohwer & Kubitzki, *Umbellularia* (Nees) Nuttall and *Urbanodendron* Mez (Rohwer, 1993a, 1993b; Chanderbali *et al.*, 2001; Trofimov, Rudolph & Rohwer, 2016). Most of these taxa are found in the Neotropics, except the North American *Umbellularia* and *c.* 40 *Ocotea* spp. from Africa and Madagascar (van der Werff, 1996, 2013).

Since the treatment of Mez (1889), *Ocotea* has been considered to be the largest genus among the Neotropical Lauraceae, currently with *c.* 400 recognized species (Rohwer, 1986; Moraes & van der Werff, 2011; van der Werff, 1996, 2002, 2011, 2013, 2017). Only a relatively small number of these have been examined in previous molecular phylogenetic studies, focused on other genera or on the major evolutionary lineages in Lauraceae (Chanderbali *et al.*, 2001; Chanderbali, 2004; Trofimov *et al.*, 2016; Rohde *et al.*, 2017). However, these studies have shown that *Ocotea* is polyphyletic. The 12 other genera of the *Ocotea* complex that have been examined already were found to be nested among species currently included in *Ocotea* (only *Gamanthera*, *Phyllostemonodaphne* and *Povedadaphne* have yet to be examined). Nevertheless, no attempt has been made to propose a phylogenetic classification. This is obviously due to two problems: (1) the large size of the group and (2) the fact that most *Ocotea* spp. with bisexual flowers have retained the plesiomorphic flower structure of the group, so that morphological synapomorphies have to be sought in vegetative characters, fruit structures or

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minor details of the flowers. Distinguishing features of evolutionary lineages in *Ocotea s.l.* are available and have been used by Rohwer (1986) to circumscribe 29 morphological groups. In addition, a recent study of epidermal features by Trofimov & Rohwer (2018) revealed a considerable diversity in stomatal shapes among *Ocotea* spp., mostly coincident with the groups defined by Rohwer (1986).

Here we report the results of a phylogenetic analysis of 123 species of the *Ocotea* complex, using nuclear and plastid markers, as a first step towards a natural classification in this species-rich group of Neotropical Lauraceae. Since the type species of *Ocotea*, *O. guianensis* Aubl. is dioecious and the dioecious clade (also including *Endlicheria* and *Rhodostemonodaphne*) has been retrieved as a monophyletic group in previous studies, whereas the remaining genera have bisexual flowers, we focus on *Ocotea* spp. with bisexual flowers here.

MATERIAL AND METHODS

Taxon sampling

We examined 123 species of the *Ocotea* complex *sensu* Chanderbali *et al.* (2001) or the *Aniba* and *Ocotea* subgroups *sensu* Rohwer (1993a), currently attributed to the genera *Aniba, Damburneya* (Trofimov *et al.*, 2016), *Dicypellium*, *Endlicheria*, *Kubitzkia*, *Licaria, Nectandra, Ocotea*, *Paraia*, *Pleurothyrium*, *Rhodostemonodaphne*, *Umbellularia* and *Urbanodendron*. Three members of the *Persea* group [*Machilus grijsii* Hance, *Persea americana* Mill. and *Phoebe sheareri* (Hemsl.) Gamble] were chosen as outgroup taxa. All specimens, their origin and collectors are listed in the Appendix. We were unable to add molecular data for the genera that have not been examined so far, either due to lack of material (*Gamanthera* and *Povedadaphne*) or because our attempts to extract and amplify DNA failed (*Phyllostemonodaphne*).

DNA extraction, polymerase chain reaction (PCR) amplification and sequencing

DNA from silica-gel dried material or from herbarium specimens was isolated with the innuPREP Plant DNA Kit (Analytik Jena, Germany) according the manufacturer's protocol, with modifications (Rohwer & Rudolph, 2005; Trofimov *et al.*, 2016).

The nuclear internal transcribed spacer (ITS) and the plastid intergenic region between the *psbA* (photosystem II protein D1) and the *trnH* (transfer RNA histidine) genes (*psbA-trnH*) were selected because a particularly high variability was expected in these regions (Kress *et al.*, 2005; Yao *et al.*, 2009; Song *et al.*, 2009; Dong *et al.*, 2012), and previous studies have shown their suitability for phylogenetic studies in Lauraceae (Trofimov *et al.*, 2016; Rohde *et al.*, 2017). The ITS region was amplified according to the general method of White *et al.* (1990) as modified by Rohwer *et al.* (2009). Because of the rather high GC content in the ITS of Lauraceae (up to *c.* 71% in our taxa), we used double amounts of dGTP and dCTP in the PCR mix. This led to an improvement in both quantity and quality of PCR products compared to the standard dNTP solution. The amplification of the plastid *psbA-trnH* spacer was carried out under the same conditions, but neither dimethylsulphoxide (DMSO) nor a modified dNTP solution was used, because of much lower GC content. The primers used for amplification and sequencing are listed in Table 1. Purification of the PCR products, sequencing reaction and precipitation of the sequencing products were

Table 1. Primers for ITS and *psbA-trnH* used in this study.

Primer	Direction	Sequence	Author
ITS			
ITS-18	F	5′-GTCCACTGAACCTTATCATTTAGAGG-3′	Käss & Wink, 1997; Beyra-Matos & Lavin, 1999
ITS-4	R	5′-TCCTCGCTTATTGATATGC-3′	White *et al.*, 1990
ITS-CL	R	5′-GCAATTCACACCAMGTATCGC-3′	Trofimov *et al.*, 2016
ITS-D	F	5′-CTCTCGGCAACGGATATCTCG-3′	Blattner, 1999
ITS-H	R	5′-CGGTTCGCTCGCCGTTACTA-3′	Rohwer *et al.*, 2014
ITS-L-400	F	5′-CGACTCTCGGCAACGGATATCTC-3′	Trofimov *et al.*, 2016
ITS-L-459	R	5′-AAGACTCGATGGTTCACGGG-3′	Trofimov *et al.*, 2016
***psbA-trnH*-region**			
psbA F	F	5′-GTTATGCATGAACGTAATGCTC-3′	Sang, Crawford & Stuessy, 1997
psbA-Lau		5′-CGAAGYTCCATCTACAAAYGG-3′	Rohwer & Rudolph, unpub.
trnH(GUG)	R	5′-ACTGCCTTGATCCACTTGGC-3′	Hamilton, 1999
trnH-A-8.1	R	5′-TGGATTCACAAATCCACTGC-3′	Klak, Bruyns & Hanáček, 2013

performed as described earlier (Rohwer *et al.*, 2014; Trofimov *et al.*, 2016).

SEQUENCE ANALYSES

The sequences were detected by an automated ABI 3500 Genetic Analyzer (Applied Biosystems, Carlsbad, USA) according to the manufacturer's instructions. The sequences were edited and consensus sequences for each species were created by using the program Sequencher 4.8 (Gene Codes Corporation, 1991–2007). All sequences were aligned by the MUSCLE algorithm, implemented in MEGA v.6.06 (Tamura *et al.*, 2013), with manual adjustments according to the principles outlined by Rohwer *et al.* (2014). Potentially informative insertions or deletions (indels) were coded in an indel matrix appended to the DNA sequence matrix, usually following the rules of simple indel coding (Simmons & Ochoterena, 2000). However, we coded multistate characters (0/1/2/3/4) to account for different combinations of bases within the same indel positions. Indels that were only ambiguously alignable were moved to uninformative positions. A micro-inversion of mostly 5 (occasionally 6) base pairs (bp) recognized in the *psbA-trnH* spacer (positions 79–86 in our *psbA-trnH* alignment) was reversed and complemented because a previous study (Rohde *et al.*, 2017) and additional unpublished results had shown that its orientation was variable, even within a species. Another region in which the observed differences among the sequences possibly might be explained by several micro-inversions of different size and slightly shifted positions (positions 298–303 in our *psbA-trnH* alignment) was excluded from the analyses.

PHYLOGENETIC ANALYSES

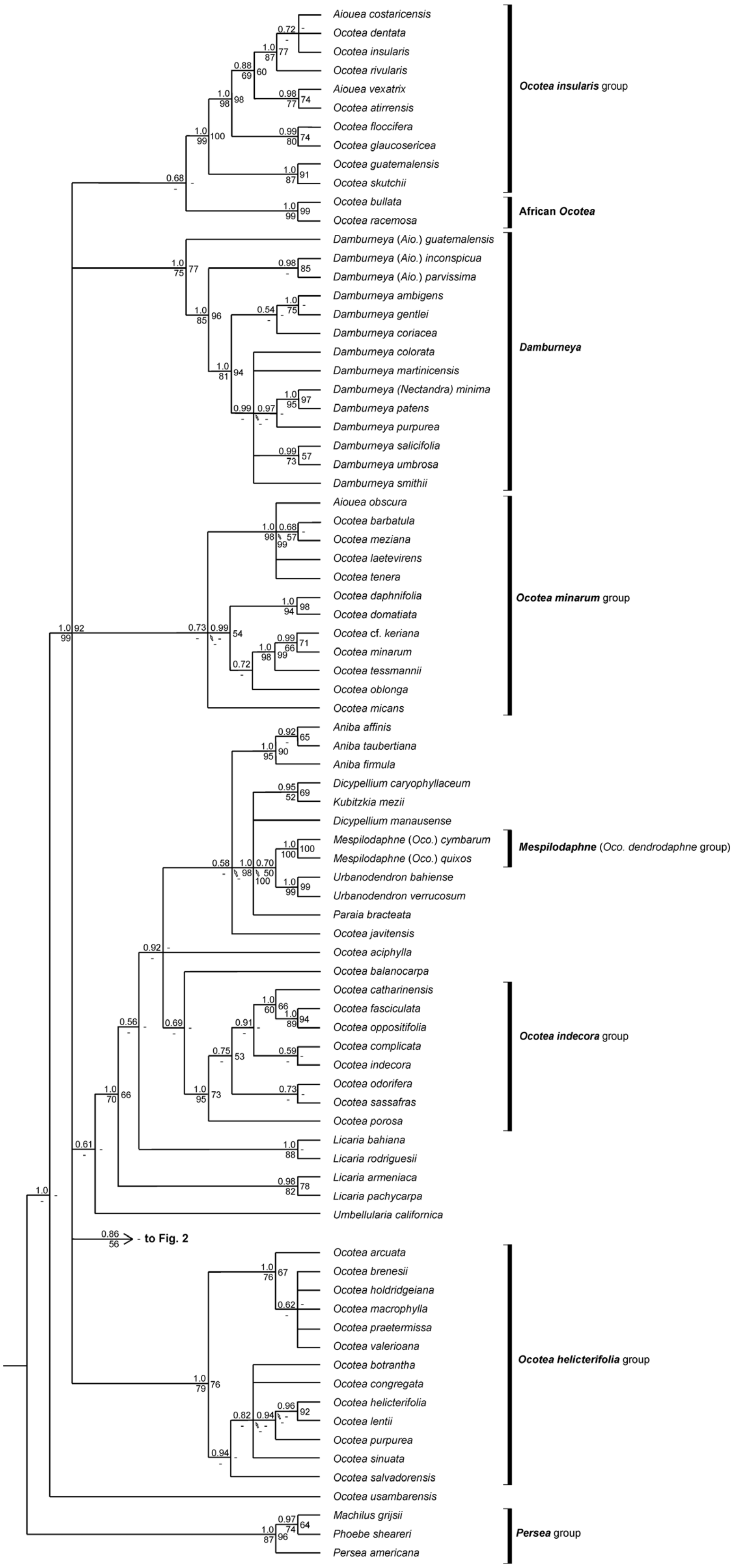
The data matrices, each consisting of 125 taxa, were analysed separately and combined using maximum parsimony (MP) in PAUP* 4.0b10 (Swofford, 2002), Bayesian inference (BI) using MrBayes 3.2.2 (Ronquist & Huelsenbeck, 2003) and maximum likelihood (ML) using TREEFINDER, version from March 2011 (Jobb, 2011). The MP analyses were performed as heuristic searches, with 100 random sequence addition replicates, tree bisection-reconnection (TBR), retaining of all minimum length trees (MULTREES = YES) and collapse of zero-length branches. Gaps were treated as missing data. When the number of trees found in the first sequence addition replicate exceeded 20 000, we limited the number of trees saved per replicate to 1000 [NCHUCK = 1000, CHUCKSCORE = (minimum length found in first attempt)]. Branch support was estimated by bootstrap analyses (Felsenstein, 1985), with the number of branch exchanges limited to one million per bootstrap replicate (rearrlimit = 1000000).

For the BI analysis, the data were separated into four unlinked partitions, (1) for the ITS1 and ITS2 regions, (2) for ITS indel codes, (3) for the *psbA-trnH* intergenic region and (4) for the *psbA-trnH* indel codes. The 5.8S rDNA region was excluded from the analysis because it did not contain any parsimony-informative position. For the partitions including DNA data, the most suitable substitution models were determined in MEGA v.6.06, according to the Bayesian information criterion (BIC). The general time reversible model was suggested for the ITS data, whereas the Tamura three-parameter model was suggested for the *psbA-trnH* spacer, both with discrete gamma distribution. Two simultaneous runs of four Metropolis-coupled Monte Carlo Markov chains (MCMCMC) were run for ten million generations for the combined dataset (five million for the individual markers), saving the current tree every 500 generations. The burn-in was determined by visual inspection of the likelihood values, visualized as a graph in Microsoft Excel 2010. The posterior probabilities for individual clades were calculated by producing a majority-rule consensus of the remaining trees in PAUP.

Two partitions were used for the ML analyses, for the ITS data and the *psbA-trnH* data. In contrast to

Table 2. Statistics according to matrix and MP analyses.

	ITS	***psbA-trnH***	**Combined**
total characters (including indels)	801	510	1311
excluded characters	166	6	172
potentially parsimony-informative indels	25	10	35
constant characters	339	393	732
parsimony-uninformative characters	109	56	165
potentially parsimony-informative characters	187	55	242
number of trees	54 000	100 000	48 000
tree length	850	173	1069
consistency index	0.494	0.717	0.509
retention index	0.787	0.866	0.780


Aiouea costaricensis
Ocotea dentata
Ocotea insularis
Ocotea rivularis
Aiouea vexatrix
Ocotea atirrensis
Ocotea floccifera
Ocotea glaucosericea
Ocotea guatemalensis
Ocotea skutchii
Ocotea insularis group
Ocotea bullata
Ocotea racemosa
African Ocotea
Damburneya (Aio.) guatemalensis
Damburneya (Aio.) inconspicua
Damburneya (Aio.) parvissima
Damburneya ambigens
Damburneya gentlei
Damburneya coriacea
Damburneya colorata
Damburneya martinicensis
Damburneya (Nectandra) minima
Damburneya patens
Damburneya purpurea
Damburneya salicifolia
Damburneya umbrosa
Damburneya smithii
Damburneya
Aiouea obscura
Ocotea barbatula
Ocotea meziana
Ocotea laetevirens
Ocotea tenera
Ocotea daphnifolia
Ocotea domatiata
Ocotea cf. keriana
Ocotea minarum
Ocotea tessmannii
Ocotea oblonga
Ocotea micans
Ocotea minarum group
Aniba affinis
Aniba taubertiana
Aniba firmula
Dicypellium caryophyllaceum
Kubitzkia mezii
Dicypellium manausense
Mespilodaphne (Oco.) cymbarum
Mespilodaphne (Oco.) quixos
Mespilodaphne (Oco. dendrodaphne group)
Urbanodendron bahiense
Urbanodendron verrucosum
Paraia bracteata
Ocotea javitensis
Ocotea aciphylla
Ocotea balanocarpa
Ocotea catharinensis
Ocotea fasciculata
Ocotea oppositifolia
Ocotea complicata
Ocotea indecora
Ocotea odorifera
Ocotea sassafras
Ocotea porosa
Ocotea indecora group
Licaria bahiana
Licaria rodriguesii
Licaria armeniaca
Licaria pachycarpa
Umbellularia californica
0.86 56 - to Fig. 2
Ocotea arcuata
Ocotea brenesii
Ocotea holdridgeiana
Ocotea macrophylla
Ocotea praetermissa
Ocotea valerioana
Ocotea botrantha
Ocotea congregata
Ocotea helicterifolia
Ocotea lentii
Ocotea purpurea
Ocotea sinuata
Ocotea salvadorensis
Ocotea helicterifolia group
Ocotea usambarensis
Machilus grijsii
Phoebe sheareri
Persea americana
Persea group

PAUP and MrBayes, indel codes cannot be used in TREEFINDER. Heuristic searches were performed with a search depth of two and 1000 replicates, using the default parameters and the models suggested by the program. Unlike MEGA, TREEFINDER suggested a transitional model (TIM = J3) for both the ITS and the *psbA-trnH* data. Likelihood bootstrap analyses were performed with 1000 replicates. In the MP and ML analyses, we considered 90% bootstrap support (BS) as significant. In the Bayesian analyses, where the support values are generally higher, we considered a posterior probability (PP) of 0.97 as significant.

RESULTS

Sequence characteristics

The statistics of the aligned ITS and *psbA-trnH* genome regions for the single and combined analyses are shown in the first six rows of Table 2. The aligned genome regions of the combined analysis have a total length of 1276 bp. We excluded 172 alignment positions from the analysis, 166 representing the uninformative 5.8S region of the ribosomal DNA and six in the region possibly affected by multiple micro-inversions in the *psbA-trnH* spacer. Of the remaining 1104 alignment positions 732 (66.3%) were constant, 165 (14.9%) were parsimony-uninformative and 207 positions (18.7%) were potentially parsimony-informative.

The alignment showed 35 potentially parsimony-informative insertions or deletions (indels), 25 in the ITS region and ten in the *psbA-trnH* spacer. Therefore, the final data matrix consisted of 1139 characters, 1104 DNA characters plus 35 indels, encoded using the numbers 0 to 4.

The results based on each single marker provided (much) less resolution and lower support values than those based on the combined dataset. Only a single case of significantly supported conflict was found between the two data sets among the dioecious species of the *Ocotea* complex. In the ITS analysis, *Endlicheria punctulata* (Mez) C.K.Allen is strongly supported as sister to a clade including *Ocotea leptobotra* (Ruiz & Pav.) Mez, *O. pauciflora* (Nees) Mez, *O. spectabilis* (Meisn.) Mez and *O. teleiandra* (Meisn.) Mez (PP 1.0), whereas *Rhodostemonodaphe parvifolia* Madriñán is strongly supported as member of a clade including also *Endlicheria chalisea* Chanderb., *E. citriodora* van der Werff, *E. longidcaudata* (Ducke) Kosterm., *E. pyriformis* (Nees) Mez, *Rhodostemonodaphne negrensis* Madriñán and *Ocotea puberula* (Rich.) Nees (PP 1.0). In the *psbA-trnH* analysis, in contrast, *Endlicheria punctulata* is strongly supported as sister to *Rhodostemonodaphe parvifolia* (PP 0.97). Here, we show only the results based on the combined data set (Figs 1, 2). The trees based on the single markers are available in the Supporting Information.

Maximum parsimony analysis

The statistics of the parsimony analyses of the single and combined markers are shown in rows seven to ten of Table 2. The parsimony analysis of the combined data resulted in 48 000 trees with a length of 1069 steps, a consistency index (CI) of 0.509 and a retention index (RI) of 0.780. Because the bootstrap trees of the MP analyses were much less resolved and supported than the trees of the BI analyses, only the results of the BI analysis of the combined data set are described in detail in this study. The MP trees (majority-rule and bootstrap consensus) based on the combined data set are available in the Supplementary Information.

The topology retrieved in the MP analysis of the combined markers is almost fully compatible with the result of the BI, except that *Aniba affinis* (Meisn.) Mez and *A. taubertiana* Mez form a moderately supported clade in the BI result (PP 0.92), with *A. firmula* (Nees & Mart.) Mez as their sister taxon, whereas *Aniba affinis* and *A. firmula* form a weakly supported clade (BS 51%) in the MP result, with *A. taubertiana* as their sister taxon. Twenty-one internal nodes, all with PP 1.0 in the BI, also reached significant support in the MP analysis.

Maximum likelihood analysis

The result of the maximum likelihood analysis and the likelihood bootstrap consensus are available in the Supplementary Information. The maximum likelihood bootstrap consensus tree is slightly less resolved than the tree resulting from the BI analysis, but its topology is fully compatible in all clades with a > 70% likelihood bootstrap support (ML-BS).

Figure 1. Results of the BI using the combined ITS and *psbA-trnH* sequence data matrix, part 1. Numbers above branches are posterior probabilities, numbers below branches are MP-BS values, numbers to the right of the nodes are maximum likelihood bootstrap values. Hyphens indicate clades with < 50% BS. The clade including the *Endlicheria*/*Rhodostemonodaphne* alliance, the dioecious *Ocotea* species, *Nectandra* and *Pleurothyrium* is shown in detail in Figure 2. *Aio.* = *Aiouea, Oco.* = *Ocotea.*

Bayesian inference

The BI of the combined dataset reached convergence at < 25 000 of ten million generations, so that 250 of the 20 001 saved trees of each run (1.25%) had to be discarded as burn-in. The final standard deviation of split frequencies oscillated around 0.009. The resulting cladogram is shown in Figures 1 and 2.

The separation between the outgroup (the *Persea* group, including *Machilus grijsii*, *Persea americana* and *Phoebe sheareri*) and the ingroup (the *Ocotea* complex) is well-supported (PP 1.0 / BS 87% / ML-BS 96%). Within the *Ocotea* complex, the African *O. usambarensis* Engl. is found as sister to the remaining taxa, which form a strongly supported group (PP 1.0 / BS 99% / ML-BS 92%).

The remaining taxa form a polytomy consisting of six clades. The first clade is poorly supported and present in the BI result only (PP 0.68). It consists mainly of Neotropical taxa placed in the *O. insularis* (Meisn.) Mez group by Rohwer (1986) and/or van der Werff (2002), plus *O. bullata* (Burch.) E.Meyer from South Africa and *O. racemosa* (Danguy) Kosterm. from Madagascar. The two Old World taxa form a strongly supported clade (PP 1.0 / BS 99% / ML-BS 99%) as sister to the similarly strongly supported *O. insularis* group (PP 1.0 / BS 99% / ML-BS 100%). The *Ocotea insularis* group clade includes not only species currently placed in *Ocotea*, but also two of the *Aiouea* spp. included in this study, *A. costaricensis* (Mez) Kosterm. and *A. vexatrix* van der Werff. The two *Aiouea* spp. do not form a clade but are nested separately among the species of the *O. insularis* group.

The second clade is well-supported in the BI analysis only (PP 1.0 / BS 75% / ML-BS 77%) and includes the genus *Damburneya* and another three species currently placed in *Aiouea*, *A. guatemalensis* (Lundell) S.S.Renner, *A. inconspicua* van der Werff and *A. parvissima* (Lundell) S.S.Renner. *Aiouea guatemalensis* appears as sister to the remaining species, which form a well-supported clade in the BI analysis (PP 1.0 / BS 85% / ML-BS 96%). The other two *Aiouea* spp. form a well-supported clade in the BI analysis only (PP 0.98 / BS < 50% / ML-BS 84%), remaining unresolved in the result of the MP analysis. *Damburneya* spp. form a clade that is the sister group to *A. inconspicua* and *A. parvissima* and well-supported in the BI and ML results (PP 1.0 / BS 85% / ML-BS 94%).

The third clade is present in the BI analysis only, and poorly supported (PP 0.73). It includes *Ocotea micans* Mez, a well-supported subclade (PP 1.0 / BS 98% / ML-BS 99%) including the Central American species *Aiouea obscura* van der Werff, *Ocotea barbatula* Lundell, *O. laetevirens* Standl. & Steyerm., *O. meziana* C.K.Allen and *O. tenera* Mez & Donn. Sm., and another subclade that is well-supported in the BI result only (PP 0.99 / BS < 50% / ML-BS 54%), consisting of predominantly South American species placed in the *Ocotea minarum* Mez group by Rohwer (1986) [*O. daphnifolia* (Meissn.) Mez, *O. domatiata* Mez, *O. keriana* A.C.Smith, *O. minarum* (Nees & Mart.), *O. oblonga* (Meissn.) Mez and *O. tessmannii* O.C.Schmidt]. Two clades within this group are well-supported in all analyses, one consisting of *O. daphnifolia* and *O. domatiata* (PP 1.0 / BS 94% / ML-BS 98%), the other consisting of *O. keriana*, *O. minarum* and *O. tessmannii* (PP 1.0 / BS 98% / ML-BS 99%).

The fourth clade is present in the BI result only (PP 0.61). It includes all examined species of the genera *Aniba*, *Dicypellium*, *Kubitzkia*, *Licaria*, *Paraia*, *Umbellularia* and *Urbanodendron*, plus several *Ocotea* spp. with bisexual flowers, most of which have been placed in the *Ocotea aciphylla* (Nees) Mez, *O. dendrodaphne* Mez or *O. indecora* (Schott) Mez groups by Rohwer (1986). *Umbellularia* appears as sister to the remaining taxa in the result of the BI analysis only. The other taxa form a clade that is strongly supported in the BI result only (PP 1.0 / BS 71% / ML-BS 66%). Among these, the species of the *O. dendrodaphne* group [*O. cymbarum* Kunth and *O. quixos* (Lam.) Kosterm.] form a well-supported subclade (PP 1.0 / BS 100% / ML-BS 100%) nested among the minor genera *Dicypellium*, *Kubitzkia*, *Paraia* and *Urbanodendron* (PP 1.0 / BS 98% / ML-BS 100%), whereas the species of the *O. indecora* group form a well-supported clade in the BI and MP analyses (PP 1.0 / BS 95% / ML-BS 73%) together with *O. catharinensis* Mez and *O. porosa* (Nees & Mart.) Barroso. The species of the *O. aciphylla* group [*O. aciphylla, O. balanocarpa* (Ruiz & Pav.) Mez, and *O. javitensis* (Kunth) Pittier] do not form a common clade but are (partly) separated by poorly supported nodes in the BI and ML results, and completely unresolved in the MP result.

The fifth clade in the polytomy is not significantly supported (PP 0.86 / BS 56% / ML-BS < 50%) and includes all dioecious taxa (*Endlicheria*, *Rhodostemonodaphne*, clearly dioecious *Ocotea* spp.), together with *Nectandra* and *Pleurothyrium* with bisexual flowers. The dioecious species form two separate, well-supported clades. The larger of these clades (PP 1.0 / BS 92% / ML-BS 89%) includes all examined species of *Endlicheria* and *Rhodostemonodaphne*, plus several dioecious *Ocotea* spp. placed in the *O. floribunda* Mez, *O. guianensis* and *O. pulchella* (Nees & Mart.) Mez groups by Rohwer (1986), two species of the *O. cernua* (Nees) Mez group, and *O. puberula* (Rich.) Nees. The two species of the *O. cernua* group, *O. divaricata* (Nees) Mez and *O. laxa* (Nees) Mez, form a strongly supported clade in the BI

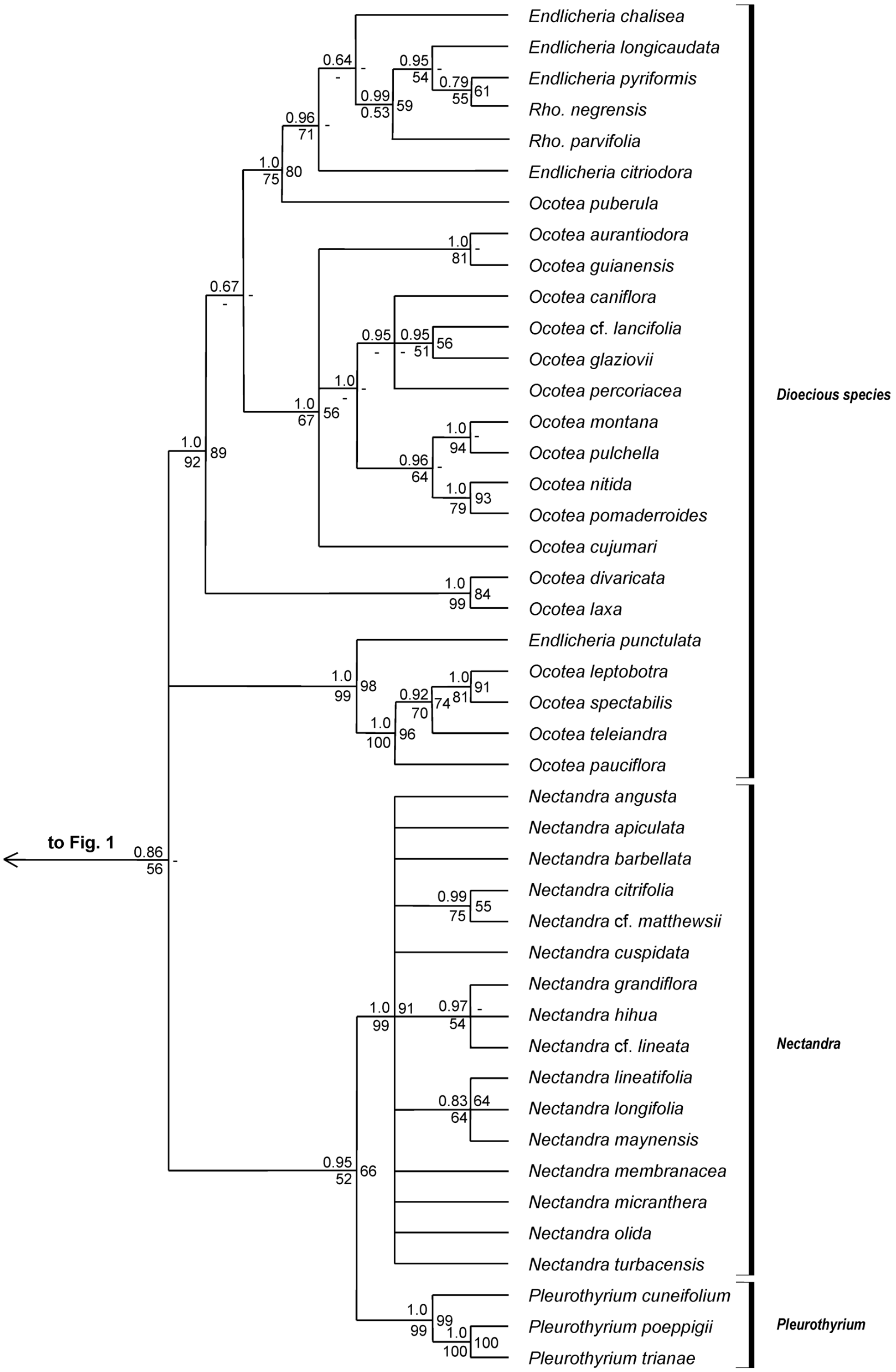


Figure 2. Results of the BI using the combined markers ITS and *psbA-trnH*, part 2. Numbers above branches are posterior probabilities, numbers below branches are MP-BS values, numbers to the right of the nodes are maximum likelihood bootstrap values. Hyphens indicate clades with < 50% BS. *Rho.* = *Rhodostemonodaphne*.

and MP results (PP 1.0 / BS 99% / ML-BS 84%) that is sister to the rest in the BI result and member of a trichotomy in the MP and ML results. The smaller dioecious clade (PP 1.0 / BS 99% / ML-BS 98%) consists of *Endlicheria punculata* (Mez) C.K.Allen as sister to the other species of the *O. cernua* group examined here. The clade consisting of *Nectandra* and *Pleurothyrium* just failed to reach the support level that we regard as significant in the BI result (PP 0.95), and it is also present in the MP and ML results, albeit without support (BS 52% / ML-BS 66%). The genera *Nectandra* and *Pleurothyrium* are well-supported as monophyletic groups (PP 1.0 / BS 99% / ML-BS 91% and PP 1.0 / BS 99% / ML-BS 99%, respectively), but *Nectandra* shows little internal resolution. The sixth clade (PP 1.0 / BS 79% / ML-BS 76%) consists of species placed in or near the *Ocotea helicterifolia* (Meisn.) Hemsl. species group by Rohwer (1986, 1991) and/or van der Werff (2002).

DISCUSSION

THEORETICAL CONSIDERATIONS

The aim of this study was to improve the classification of the *Ocotea* complex, in which the genus *Ocotea* has been known to be paraphyletic for almost 20 years. Much has been written about the merits of recognizing paraphyletic taxa vs. monophyletic taxa only (see, e.g. Hörandl & Stuessy, 2010 vs. Schmidt-Lebuhn, 2012), and there is no point in repeating all of that here. Relevant for our discussion are mainly the arguments brought forward by Schmidt-Lebuhn (2012) to rebut the statement 'members of a paraphyletic group are unaffected by the evolution of a nested descendant.' His conclusion was that 'Of course no group ever becomes paraphyletic, for the simple reason that it always includes the nested new (sub)group!' While this is obviously correct, it does not answer the question as what those (still extant) species of the ancestral group should be treated that are not members of any nested clade with clear synapomorphies. Schmidt-Lebuhn (2012) discussed this problem mainly in the context of fossils, but recognized that it may lead to a real conflict between phylogenetic and Linnaean classification when a species must be assigned to a genus. For practical purposes, we have to deal with the requirements of both, phylogenetic classification and the provisions of the *International Code of Nomenclature* (Turland *et al.*, 2018). If we had to devise a classification *de novo*, we would certainly not propose a genus *Ocotea* in its current circumscription. This, however, is a purely hypothetical option. Therefore, we concentrate on a more practical question: which attributes should a group have in order to be split off as a separate genus?

1. The group must be monophyletic. This is the most important paradigm of phylogenetic systematics, and a necessary but by no means sufficient condition. We decided a priori to accept support values of ≥ 90% BS AND PP ≥ 0.97 as significant, but in fact all 21 clades with ≥ 90% BS have PP 1.0 in our results.
2. The group must be recognizable morphologically. This requirement can be phrased in three different ways: (a) The group must have morphological synapomorphies. This may sound like the most stringent demand, but phylogenetic classification does allow reversals within a clade, so that not all members need to show the synapomorphy of the group. (b) The group must have a combination of characters allowing it to be separated from all other genera. This demand is less stringent in that it does not differentiate between plesiomorphic and apomorphic characters, but more stringent in that it requires the presence of this character combination in all members of the group. (c) The group must be recognizable with some experience. This is certainly the least stringent demand, but many traditional genera have been shaped that way. We believe that any of these is a valid option (in addition to criterion 1), even (c). If a group can be recognized, it means that it must have some characters that allow this recognition, even if so far it cannot be described either as a clear synapomorphy or a unique combination of characters.
3. The group can be shown to be closer to a different accepted genus than to the clade that comprises the type species of the genus in which the group is currently placed. This is a strong argument, perhaps the one that is most frequently used in the literature, but of course it implies that the accepted genera deserve this rank. For the purpose of the present paper, we use this criterion as a necessary condition, i.e. we do not (yet) propose new genera for clades fulfilling criteria 1 and 2 if we cannot show with confidence that they fulfil this criterion as well.
4. Stuessy & König (2008) suggested that also the patristic distance should be taken into account, i.e. clades separated by a particularly long branch from their next more inclusive group may also be separated. In our opinion, this rationale can at best provide supporting evidence, because long branches may arise from disparate processes such as rapid divergence, incomplete or biased sampling of taxa or characters, or extinction of taxa that would have broken up these branches. Nevertheless, the branch lengths will be mentioned where this appears appropriate.

OVERALL TOPOLOGY

Our results show many similarities to an earlier study of Lauraceae by Chanderbali *et al.* (2001). Their study was based entirely on ITS sequences, and in our study the ITS sequences contribute 77% of the informative characters. Several genera and a few species groups in *Ocotea* were retrieved as monophyletic and well-supported in both studies. These groups are the genera *Aniba*, *Nectandra* (*s.s.*), *Pleurothyrium* and *Urbanodendron*, a clade consisting of the recently reinstated genus *Damburneya* (Trofimov *et al.*, 2016; well-supported as the *Nectandra coriacea* (Sw.) Griseb. species group in Chanderbali *et al.*, 2001) plus three species still treated as *Aiouea*, even though they do not fit a recent re-circumscription of this genus (Rohde *et al.*, 2017), as well as the *Ocotea dendrodaphne*, *O. helicterifolia* and *O. insularis* species groups. Within the *Ocotea* complex, further similarities include the presence of (1) a clade consisting of all species of *Rhodostemonodaphne* and *Endlicheria* except *E. punctulata*, nested in (2) a clade including nearly all (obviously) dioecious species, except those of the *O. cernua* group, irrespective of whether they are currently placed in *Endlicheria, Ocotea*, or *Rhodostemonodaphne*. The dioecious taxa are parts of the same clade (3) as another clade including *Nectandra* and *Pleurothyrium* (4), both with bisexual flowers, like nearly all other taxa of the *Ocotea* complex. Differences between the study of Chanderbali *et al.* (2001) and ours are restricted to clades without significant support.

Unfortunately, we have not been able to improve the resolution at the base of the *Ocotea* complex by adding *psbA-trnH* sequences. Therefore, the positions of the major clades relative to one another remain uncertain. In our results, we see a polytomy at the base of the *Ocotea* complex. The result of Chanderbali *et al.* (2001) looks more resolved, but like in our study only very few of the nodes (and generally the same ones) reached significant support.

DIOECIOUS SPECIES OF THE *OCOTEA* COMPLEX

It may be appropriate to discuss the morphologically clearly dioecious clades within the *Ocotea* complex first, because the type species of *Ocotea*, *O. guianensis*, is such a species. Its staminate flowers possess a slender pistillode that does not contain an ovule, but still possesses a stigma. The pistillate flowers have nine staminodes with rudimentary, empty pollen sacs. Staminodes of the fourth androecial whorl, which are common among the hermaphrodite species of the *Ocotea* complex, are usually absent in the dioecious species, rarely rudimentary and stipitiform. This may be due to the fact that their function as nectar secreting organs during the female flowering phase of heterodichogamous species (Rohwer, 2009) has become obsolete with dioecy. Mostly it appears to be clade-specific whether or not the pistillode of staminate flowers still has a stigma (e.g. present in the *O. guianensis*, *O. pulchella* and *O. floribunda* groups, absent in the *O. cernua* and *O. corymbosa* groups as well as in most species of *Endlicheria* and *Rhodostemonodaphne*), but Rohwer (1986) noted that some species are variable in this respect [e.g. *Ocotea dispersa* (Nees) Mez and *O. amazonica* (Meisn.) Mez]. In our study, we found two separate dioecious clades arranged in a trichotomy with a clade including *Nectandra* and *Pleurothyrium*. In previous studies (Chanderbali *et al.*, 2001; Chanderbali, 2004) they formed a single clade, but without BS. The inclusion of *Endlicheria punctulata* in the *O. cernua* group (the smaller of the dioecious clades) already has been discussed by Chanderbali (2004). Morphologically, it is particularly similar to *Ocotea pauciflora* (Nees) Mez in its pauciflorous inflorescences, sparsely pubescent flowers, and glabrous concolorous leaves with immersed venation below (Chanderbali, 2004). In fact, the two taxa are so similar to one another that *E. punctulata* might be considered synonymous with *O. pauciflora*. This would not be the only case of variation in the number of pollen sacs per anther within a single species (see discussion in Rohde *et al.*, 2017).

Ocotea guianensis is a member of the larger dioecious clade. Within this clade, the remaining species of *Endlicheria* and *Rhodostemonodaphne* form a rather closely knit alliance on the basis of morphological as well as molecular data (Chanderbali *et al.*, 2001; Chanderbali, 2004). *Endlicheria* differs from dioecious *Ocotea* and *Rhodostemonodaphne* mainly in having two rather than four pollen sacs per anther (Rohwer, Richter & van der Werff, 1991; van der Werff, 1991), a character that by itself is not sufficient to differentiate between genera (see discussion in Rohde *et al.*, 2017). *Ocotea* and *Rhodostemonodaphne* differ in the arrangement of the four pollen sacs, in two superposed pairs in *Ocotea* vs. collateral in a single row in *Rhodostemonodaphne*.

The dioecious species of the *Ocotea* complex are not the focus of this study, therefore only relatively few of them have been included in the present data set. Nevertheless, the morphological species groups described by Rohwer (1986) were to some extent retrieved here. *Ocotea caniflora* Mez, *O. glaziovii* Mez, *O. lancifolia* (Schott) Mez and *O. percoriacea* Kosterm., which form a common clade here, all have been placed in the *O. floribunda* group. *Ocotea leptobotra* (Ruiz & Pav.) Mez, *O. pauciflora*, *O. spectabilis* (Meisn.) Mez, and *O. teleiandra* (Meisn.) Mez all have been placed in the *O. cernua* group. In this case, however, two species placed in this group as well by Rohwer (1986), *O. divaricata* and *O. laxa*, form a separate clade here. The species placed in the *O. guianensis* group [*O. aurantiodora* (Ruiz & Pav.) Mez, *O. cujumary* Mart., *O. guianensis* and *O. nitida* (Meisn.) Rohwer] and in the *O. pulchella* group [*O. montana* (Meisn.) Mez, *O. pomaderroides* (Meisn.) Mez and *O. pulchella*] appear mixed in the present result, with the species of the *O. floribunda* group nested among them.

BISEXUAL SPECIES OF THE *OCOTEA* COMPLEX

Among the species with (predominantly) morphologically bisexual flowers, four of the species groups described by Rohwer (1986), the *O. dendrodaphne*, *O. helicterifolia*, *O. insularis* and *O. minarum* groups, have been retrieved with significant support among the bisexual species included here. Monophyly of the *O. minarum* group was supported in the BI result only, but its core species (*O. keriana*, *O. minarum* and *O. tessmannii*) form a well-supported clade in the MP and ML results as well. The *O. indecora* group was retrieved almost as circumscribed morphologically, with the addition of *O. catharinensis* and *O. porosa*, which had been placed near this group by Rohwer (1986). The positions of these groups relative to each other, however, remain largely uncertain. Therefore, it seems best to discuss them separately.

The Ocotea insularis *group*

The species of the *O. insularis* group usually have relatively thick branches (3–6 mm diam. 5 cm below terminal bud) that are longitudinally ridged and sometimes hollow. Their leaves are often somewhat clustered near the tips of the branchlets, often widest above the middle (obovate to oblanceolate), less frequently oblong, elliptic or lanceolate, often with an abruptly (short-) acuminate tip and a cuneate and/or revolute base. Young leaves are usually sericeous at least on the abaxial surface, but often glabrescent towards maturity. Most species have tufts of erect hairs in the axils of the secondary veins on lower leaf surface. The flowers are bisexual and arranged in sturdy, usually many-flowered inflorescences in which the second and higher order branches are flattened, with the axis of flattening in each branching order perpendicular to that in the preceding order. The tepals are usually obliquely erect at anthesis. Most characteristic compared to other *Ocotea* taxa are the stamens, with distinct filaments and roundish-trapeziform anthers (Fig. 3A, B) bearing dense patches of short, papillae-like trichomes at the junction of filament and anther, laterally and in the centre below/between the lower pollen sacs. In contrast to most other Lauraceae with bisexual flowers, staminodes of the fourth androecial whorl are absent or only irregularly occurring and minute. The fruits have a more or less cup-shaped cupule with a single margin, often bearing remnants of tepals (almost) until maturity (Fig. 4A). The group thus appears well-characterized morphologically, although hardly any of these characters are exclusive to this group or could be regarded as synapomorphies, except perhaps the characteristic trichome pattern on the stamens (but see below). In the result of the ML analysis, it is separated from the other taxa by a relatively long internal branch, the third longest in the *Ocotea* complex. Although all this may be interpreted as evidence in favour of recognizing the *O. insularis* group as a separate genus, there is one decisive point that keeps us from taking this step: its position relative to the other clades is not yet stable. In most of our analyses it is unresolved, only in the result of the BI analysis of the combined data it appears as sister to two Old World *Ocotea* spp., *O. bullata* from South Africa and *O. racemosa* from Madagascar. In the BI analysis of the ITS data alone it forms a clade with the *O. minarum* group and several species attributed to the *O. insularis* group by van der Werff (2002) based on morphological characters, which appear closer to the *O. minarum* group in the BI analysis of the combined data in our study (see below).

As in earlier studies (Chanderbali *et al.*, 2001; Rohde *et al.*, 2017), species traditionally placed in *Aiouea* (*A. costaricensis* and *A. vexatrix*) were found nested among the species of the *Ocotea insularis* group. Their similarity to the other members of this group was discussed already by van der Werff (1988) and by Rohde *et al.* (2017). However, it would make little sense to transfer them to *Ocotea* now, because it is quite likely that the group will not remain in that genus in the long run. In the study of Chanderbali *et al.* (2001), *Ocotea insularis* (Meisn.) Mez and *Aiouea costaricensis* had been placed in a species group labelled '*Licaria* group and allies', albeit without support. Most of the other members of that group share cupules with double margins, one appressed to the berry, the other more or less spreading. This character is not found among the species of the *O. insularis* group, and we therefore assume that the topology found by Chanderbali *et al.* (2001) may have been an artefact of insufficient information content.

As mentioned above, the *O. insularis* group appears as sister to two Old World *Ocotea* spp. in the result of the BI analysis of the combined data set, whereas another African species, *O. usambarensis* is strongly supported as sister to the entire rest of the *Ocotea* complex, separated by the longest internal branch in the ML analysis. However, the Palaeotropical species are poorly represented in our taxon sample, as they were in the previous studies. We will therefore defer a more detailed discussion of the Palaeotropical species to a subsequent paper.

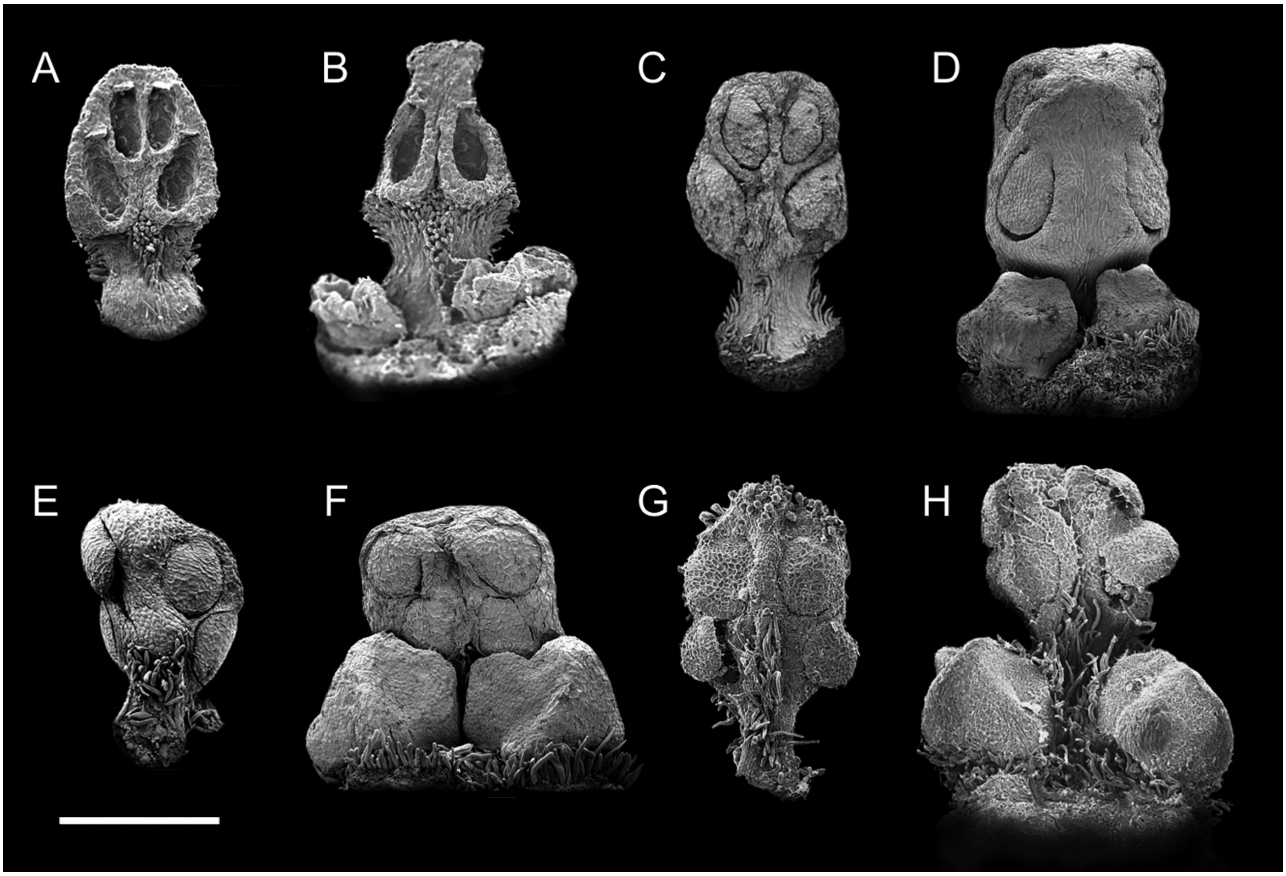


Figure 3. Outer (first or second whorl, A, C, E, G) and inner (third whorl) stamens with glands (B, D, F, H) of some species of the *Ocotea* complex examined in this paper. **A, B,** *Ocotea atirrensis* [*Jiménez 1014*]; C, D, *Ocotea oblonga* [*Herrera 3342*]; E, F, *Ocotea complicata* [*Moraes 2999*]; G, H, *Ocotea fasciculata* [*H. D. Clarke 8099*]. Scale bar = 500 µm.

The Damburneya *clade*

Damburneya, formerly known as the *Nectandra coriacea* group (Rohwer, 1993b), was reinstated by Trofimov *et al.* (2016), because it is not the closest relative of *Nectandra*. In the present analysis three species currently recognized as *Aiouea guatemalensis*, *A. inconspicua* and *A. parvissima* form a monophyletic group with *Damburneya*. The three '*Aiouea*' species were excluded from *Aiouea* by Rohde *et al.* (2017), because they do not show the typical staminodes of that genus, with a cordate or sagittate glandular head. In our study, they form a grade at the base of *Damburneya*. Therefore, it does not make sense to describe a new (paraphyletic) genus for these species, even though their anthers have only two pollen sacs, in contrast to four in the other *Damburneya* spp. The number of pollen sacs is variable in many genera of Lauraceae and even within several species (discussed in Rohde *et al.*, 2017). However, in the other cases documented so far it seems that a reduction in the number of pollen sacs from four to two occurred in several terminal lineages. Here, in contrast, the topology suggests a reversal from two to four in *Damburneya*. In their vegetative characters, especially their somewhat lustrous leaves with reticulate tertiary venation almost equally raised on both sides, these '*Aiouea*' species look like *Damburneya* spp. anyway. Their fruits, with a cupule gradually merging into the pedicel, are compatible with *Damburneya* as well. It is quite likely that fruiting material (at least of *A. guatemalensis* and *A. inconspicua*) has been filed under names of the former *Nectandra coriacea* group in many herbaria. In addition to the difference in the number of pollen sacs, the flowers of these '*Aiouea*' species also differ from most *Damburneya* spp. by fewer or no papillae on the adaxial surface of the tepals. However, in a few *Damburneya* spp., especially in *D. patens* (Sw.) Trofimov, the adaxial side of the tepals can also be sparsely papillose or glabrous.

The Ocotea minarum *group and possibly related taxa*

The study of Chanderbali *et al.* (2001) did not include any species of the *O. minarum* group. Here several

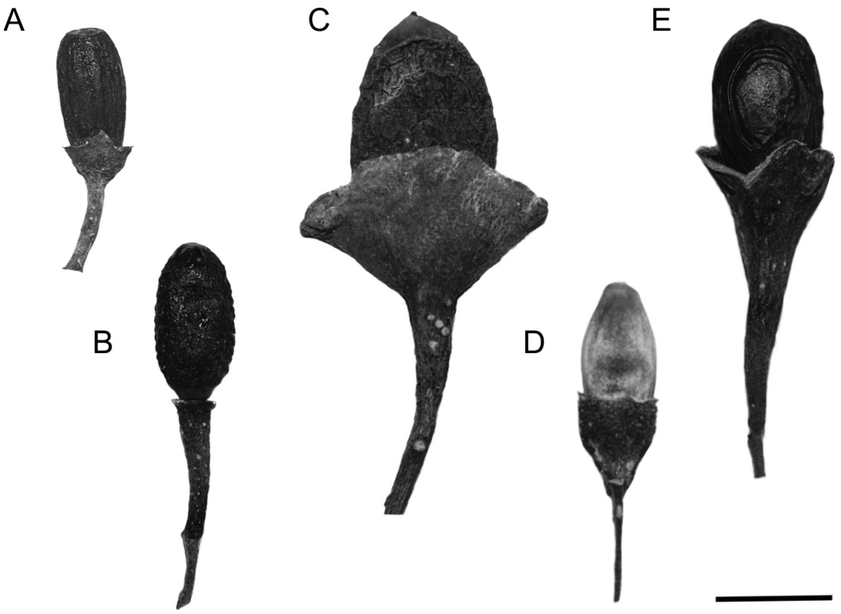


Figure 4. Fruits of some examined *Ocotea* complex species (from herbarium material). A, *Ocotea insularis* [*W. C. Burger 12181*]; B, *Ocotea oblonga* [*van der Werff 16470*]; C, *Ocotea cymbarum* [*Aymand 5542*]; D, *Ocotea fasciculata* [*Silva 2211*]; E, *Ocotea helicterifolia* [*Miller 2943*]. Scale bar = 10 mm.

of its core species (*O. daphnifolia*, *O. domatiata*, *O. keriana*, *O. minarum*, *O. oblonga* and *O. tessmannii*) form a well-supported clade in the results of the BI analyses only (individual and combined markers), but not in the MP and ML results. The species of the *Ocotea minarum* group have oblanceolate to lanceolate or elliptic leaves, which can be glabrous or variously pubescent, but in most species at least the youngest leaves are more or less sericeous on the abaxial surface. A few species, however, have erect pubescence. Most of the core species of this group have pit domatia in the axils of the secondary veins and sometimes also elsewhere on the lower leaf surface (Fig. 5E), buldging on the adaxial side. The inflorescences have a slender peduncle, usually less than half the diameter of the twig from which they originate, and they are usually relatively few-flowered, with only one or two orders of branching. In the core species of this group there are two types of flowers, apparently bisexual (functionally male?) and clearly female, in different individuals. The stamens (and staminodes of the three outer androecial whorls in female flowers) have a distinct filament, shorter than to almost as long as the anthers, which are ovate, roundish-trapeziform or almost rectangular (Fig. 3C, D), without any papillae. In normally developed flowers there are no staminodes of the fourth androecial whorl. The pistil is inserted on a small and shallow receptacle, and it has a well-developed ovule, style and stigma. There is usually no obvious difference in size or morphology between the ovaries of female and apparently bisexual flowers. The fruit is an ovoid to ellipsoid berry, almost free on a more or less conical, cylindric or knob-like swollen pedicel, in fresh material usually without a noticeable cupule (Figs 5C, H, 4B), in dried material sometimes becoming funnel-shaped by shrinking of the pedicel, resulting in a rather shallow cupule on an only slightly conically enlarged pedicel, usually without remnants of tepals. The *O. minarum* group thus can be considered well-characterized morphologically, but as in the *O. insularis* group most of these characters also occur in other groups, except perhaps the characteristic swollen pedicel in fruit. Again it is mainly the uncertain position with respect to other clades that keeps us from recognizing the *O. minarum* group as a separate genus.

In the result of the BI analysis of the combined data, it is placed in a trichotomy with *O. micans* Mez and a clade consisting of five Central American species. Two of them (*O. barbatula* and *O. tenera*) had been placed in the small *O. effusa* (Meisn.) Hemsl. group by Rohwer (1986), who had not seen *O. laetevirens* at that time, whereas three (*O. barbatula*, *O. laetevirens* and *O. meziana*) had been placed in the *O. insularis* group by van der Werff (2002). Their pattern of pubescence on the stamens is indeed similar to that of the *O. insularis* group, although the trichomes, like all other parts of the plants, appear less robust than in the core species of that group. The species of the Central American clade discussed here differ from the species of the

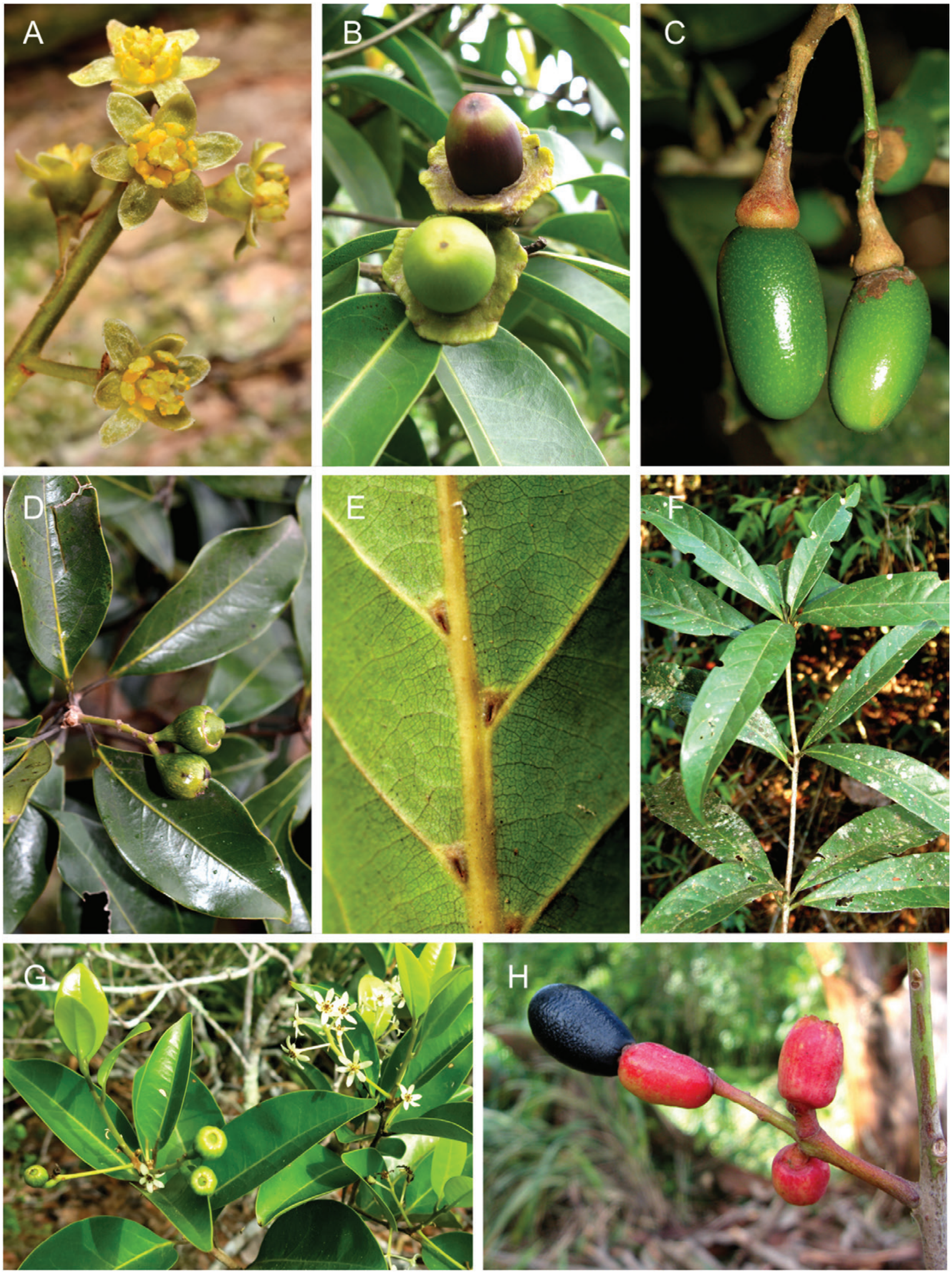


Figure 5. A, Flowers of *Ocotea porosa*; B, Almost mature fruits of *Ocotea calliscypha* L.C.S. Assis & Mello-Silva (presumably *O. indecora* group); C, Almost mature fruits of *Ocotea daphnifolia*; D, Immature fruits of *Ocotea elegans*; E, Detail of lower leaf surface of *Ocotea domatiata*, with domatia in the axils of the secondary veins; F, Branch of *Ocotea odorifera*; G, Branch with flowers and young fruits of *Ocotea arenicola* L.C.S.Assis & Mello-Silva (presumably *O. indecora* group); H, Mature fruit of *Ocotea minarum*. Photographs by J.G. Rohwer (A, C–F) and P.L.R. de Moraes (B, G–H).

O. insularis group by slender twigs, more delicate inflorescences and rather flat cupules on distinctly swollen pedicels. These cupules can be seen as an intermediate step towards knob-like cupules (Fig. 5C) or only swollen pedicels as they are found in the core species of the *O. minarum* group. At least in *O. tenera* the cupule-like structure appears to be an artefact of drying; the fruit illustrated by González & Hammel (2007) shows a naked berry on a swollen pedicel only, as in the core species of the group. A fruit on a swollen pedicel only, without a distinct cupule is also found in *O. micans* Mez. It differs in that respect from *O. guianensis*, with which it had been tentatively linked by Rohwer (1986). In addition, Juan Penagos Zuluaga (pers. comm.) has drawn our attention to the fact that *O. micans* is morphologically gynodioecious, with clearly female and apparently bisexual flowers, as in the core species of the *O. minarum* group. The shape of its stomatal complexes is also more similar to those of the *O. minarum* group than to *O. guianensis* (Trofimov & Rohwer, 2018). Gynodioecy also has been reported for *O. tenera*, a member of the Central American clade (Gibson & Wheelwright, 1996), but the trees with morphologically hermaphrodite flowers produced few or no fruits, so that they should be considered as functionally (almost completely) male. Another feature of the core species of the *O. minarum* group, pit domatia in the axils of the secondary veins on the lower leaf surface, is also known from *O. barbatula*, *O. meziana* and the fifth species of the Central American clade, *Aiouea obscura*. Most species of the *O. insularis* group have patches of trichomes in the axils of the secondary veins on lower leaf surface, but they do not have pits distinctly immersed in the mesophyll or even buldging on the upper leaf surface. Pit domatia do occur, however, also among the species of the *O. indecora* clade (see below), most pronounced in *O. catharinensis* and *O. porosa*. In the result of the BI analysis of the ITS data only, the *O. insularis* group appears to be nested among the species of the *O. minarum* group, albeit without significant support, in a trichotomy with the smaller Central American clade (*Aiouea obscura*-*Ocotea tenera*). A close relationship of the these groups appears plausible also from morphology, based on similar flower and stamen shapes, frequent absence of staminodes of the fourth androecial whorl, leaves often widest above the middle, with a cuneate to attenuate, sometimes involute base and usually sericeous pubescence on young leaves.

The ‘Licaria *group and allies’ clade*

Except for the species of the *O. insularis* group, the clade called ‘*Licaria* group and allies’ by Chanderbali *et al.* (2001) is also present in our results with considerable support at least in the BI analysis of the combined data. This clade includes most of the medium-sized and small genera of the *Ocotea* complex, most of them characterized by conspicuous autapomorphies or synapomorphies. Most species of this clade share a deep receptacle, and many of them have double-rimmed cupules. The latter are found in all species of the subclade consisting of *Dicypellium*, *Kubitzkia*, *Paraia*, *Urbanodendron*, *Ocotea cymbarum* and *O. quixos*, in nearly all *Licaria* spp., some species of the *O. indecora* group (e.g. *O. calliscypha* L.C.S.Assis & Mello-Silva, Fig. 5B), and a few *Aniba* spp., but not in the taxa of the *O. aciphylla* group. It is, therefore, uncertain if double-rimmed cupules are a synapomorphy of this clade that has been lost again in some species or if they have evolved in parallel in several lineages.

Compared to the analysis of Chanderbali *et al.* (2001), there are only minor differences in the internal topology of the group. The genus *Aniba,* the *Ocotea dendrodaphne* group and *Urbanodendron* were retrieved as well-supported clades in both the study of Chanderbali *et al.* (2001) and in ours. *Licaria* formed a well-supported clade in the result of Chanderbali *et al.* (2001), whereas in our BI results its species appear in two clades separated by a node with negligible support. As *Licaria* is a morphologically well-characterized genus, the result of Chanderbali *et al.* (2001) appears more credible in this respect. *Ocotea rhynchophylla* (Meisn.) Mez [in the *O. aciphylla* group; treated as synonym of *Ocotea aciphylla* (Nees) Mez by Rohwer (1986)] and *O. odorifera* (Vell.) Rohwer (*O. indecora* group) appear as subsequent sister taxa to *Aniba* in the study of Chanderbali *et al.* (2001), whereas in our study six taxa of the *O. indecora* group form a well-supported clade together with *O. catharinensis* and *O. porosa*, which were not placed in the *O. indecora* group by Rohwer (1986), but close to it. The taxa of the *O. aciphylla* group are separated by nodes with negligible support, if resolved at all. This last-mentioned group certainly needs additional study.

The *O. dendrodaphne* group was recognized as *Ocotea* subgenus *Dendrodaphne* by Mez (1889). Its species differ considerably from all other taxa in the *Ocotea* complex, mainly by their large flowers with tongue-shaped, heavily papillose stamens (Fig. 6A, B), with four locules in two pairs, one above the other, and by their distinctly double-rimmed cupules (Fig. 4C), with spreading outer margin. Large flowers and heavily papillose stamens occur also in *Nectandra* and in the *O. helicterifolia* group (Fig. 6E, F), but these taxa do not have double-rimmed cupules. In addition, the pollen sacs are arranged almost in a horizontal row in *Nectandra*, and the species of the *O. helicterifolia* group with similar stamens have densely hirsute

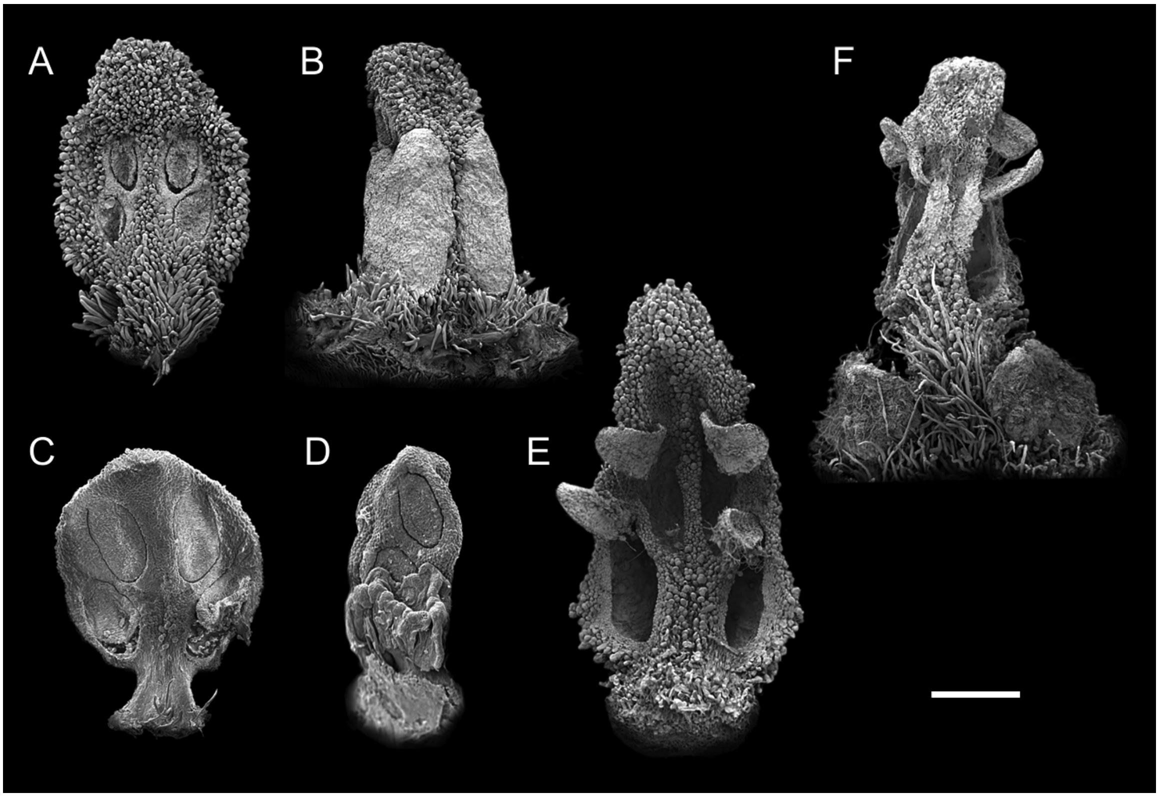


Figure 6. Outer (first or second whorl, A, C, E) and inner (third whorl) stamens with glands (B, D, F) of some species of the *Ocotea* complex examined in this paper. A, B, *Ocotea cymbarum* [*Kubitzki 75–99*]; C, D, *Ocotea helicterifolia* [*Campos 1328*]; E, F, *Ocotea sinuata* [*W. C. Burger 12086*]. Scale bar = 500 µm.

leaves and inflorescences, in contrast to invariably (sub)glabrous leaves in the *O. dendrodaphne* group. Our analyses show that the *O. dendrodaphne* group is closer to *Dicypellium*, *Kubitzkia*, *Paraia* and *Urbanodendron* than to the clade containing the type of *Ocotea*. We therefore will raise the rank of this group from subgenus to genus. It may be noticed that the *O. dendrodaphne* group is separated from the rest of the taxa by the second longest internal branch in the *Ocotea* complex, but in this case this may be due to the small number of species examined.

The second group within the '*Licaria* group and allies' clade that needs to be discussed is the clade consisting of the *O. indecora* group plus *O. catharinensis* and *O. porosa*. Most of its species differ in several characters from the plesiomorphic condition in Cinnamomeae, such as crowded leaves and consequently subverticillate branching (Fig. 5F), inflorescences crowded below the terminal bud, tepals that are rotately spreading at anthesis (Fig. 5A) and conspicuously pubescent on the adaxial side, stamens with short, densely pubescent filaments (Fig. 3E–H) and often somewhat papillose anthers (Fig. 3G, H), clavate staminodes with a distinctly glandular tip (but not a cordate or sagittate head, like in the outgroups), or a rather deep receptacle enclosing the maturing fruit for a long time (Fig. 5D, G), but only its base at maturity (Figs 4D, 5B). None of these characters, however, is entirely constant within or confined to this group. Nevertheless, the *O. indecora* group has been recognized by several authors (Baitello & Marcovino, 2003; Moraes, 2008; Assis, 2009; Assis & Mello-Silva, 2010; Moraes & van der Werff, 2011; Brotto & Baitello, 2012; Moraes, 2012; Moraes & Falcade, 2015). At the micromorphological level, it appears to be characterized by sinuate anticlinal cell walls in both the upper and the lower leaf epidermis combined with bat-shaped stomatal ledges (Trofimov & Rohwer, 2018). The *O. indecora* group was examined by Assis (2009) using morphological and molecular methods, but the results were not quite conclusive. Surprisingly, the group did not even turn out as monophyletic in the result of his ITS analysis. Only after adding morphological data to his matrix did the entire '*Licaria* group and allies' clade turn out to be in a similar composition to the analysis by Chanderbali *et al.* (2001) and to ours. Our analysis strongly suggests that the *O. indecora* group is at least closer to *Licaria*, perhaps also to *Aniba*, than to the clade containing the type of *Ocotea*, but the evidence is not quite as conclusive as in the case of the *O. dendrodaphne* group. The only species included in the analysis of

Chanderbali *et al.* (2001), *O. odorifera*, appeared closer to *Aniba* than to *Licaria* in their study, albeit without significant support. Therefore, the affinities of this group cannot yet be considered fully resolved.

The Ocotea helicterifolia *group*

The *O. helicterifolia* group was also retrieved with high support in both studies. In the study of Chanderbali *et al.* (2001) it is moderately supported as sister to a clade including *Nectandra*, *Pleurothyrium* and the dioecious taxa, whereas in our study it is unresolved with respect to that clade and four others. The topology retrieved by Chanderbali *et al.* (2001) appears quite plausible, as there are some shared characters in the *O. helicterifolia* group and *Nectandra s.s.*, such as brilliantly white, relatively large flowers (7–18 mm in diameter in the *O. helicterifolia* group) with papillose tepals and/or anthers. As in *Nectandra*, the tepals are spreading at anthesis, but this feature is also common among the species of the *O. indecora* group. The tepals are mostly glabrous or sparsely pubescent abaxially and usually papillose adaxially, and they mostly dry black. The stamens have short but mostly distinct filaments, but occasionally the anthers are subsessile. The anthers can be glabrous or heavily papillose, more or less rectangular to ovate, with a truncate to acute sterile tip (Fig. 6C–F). Staminodes of the fourth androecial whorl are mostly present, usually with a glandular patch near the tip on adaxial side, but sometimes they seem to have been fused with the filaments of the adjacent stamens or with the adjacent glands, or they can be small and hidden among trichomes and papillae, so that they are easily overlooked. The cupule of the fruit can be cup- or trumpet-shaped (Fig. 4E), or almost flat, with a single margin. The group is quite variable in its vegetative characters, but many species have a conspicuous erect pubescence on twigs, leaves and inflorescences. Sericeous pubescence, like in the *O. insularis* and *O. minarum* groups, is not found in this group. Even though the group has neither a clear synapomorphy nor an exclusive combination of characters, it has been recognized, e.g. by van der Werff (1999, 2002), who added several species to this group. A possible micromorphological synapomorphy, namely a rhombic shape of the stomatal complex, was recently described by Trofimov & Rohwer (2018), but this character is shared with the *O. minarum* group, and the relationship between these two groups (and the other major clades) remains uncertain.

CONCLUSIONS

Our results confirm those of earlier studies indicating that *Ocotea* is paraphyletic with respect to several other Neotropical genera. The taxa currently placed in *Ocotea* largely retained the plesiomorphic flower construction of Cinnamomeae, except for a tendency to reduce the size of the staminodes in the fourth androecial whorl. The evolutionary lineages therefore need to be characterized by other characters, often by a combination of fruit characters, vegetative characters and less conspicuous floral characters. The fact that most of the clades retrieved here correspond to species groups that the senior author defined based on morphological characters > 30 years ago (Rohwer, 1986) shows that these lineages are real phylogenetic units that can be recognized morphologically. In addition, we have recently shown that many of these lineages show a characteristic structure of their stomatal apparatus (Trofimov & Rohwer, 2018). In the present study, we tried to include representatives of all of the major species groups proposed by Rohwer (1986), at least of those with bisexual flowers. We have to concede, however, that we have not yet sampled representatives of several minor groups, species not placed in a morphological group, and many of the new species described over the past 30 years. We expect that additional evolutionary lineages will emerge when these species are examined. They will probably be weakly characterized morphologically (otherwise they would have been recognized earlier), but if we aim at a phylogenetic classification, the alternative would be to lump all Neotropical Cinnamomeae except *Aiouea* into *Ocotea*. This is not an option, because the other genera nested in *Ocotea* in the traditional sense are quite distinctive. However, it may be necessary to sequence whole plastid genomes and additional nuclear genes in order to break up the basal polytomy in the *Ocotea* complex.

The only entity that we can separate now with a clear conscience is the one previously recognized as *Ocotea* subgenus *Dendrodaphne* by Mez (1899). For nomenclatural reasons explained below, it will have to be called *Mespilodaphne*, a name originally applied to the *O. indecora* group and a few additional taxa by Nees (1833, 1836) and Meissner (1864).

TAXONOMIC TREATMENT

I. *Damburneya* Raf., Sylva Tellur. 136 (1838).

Type: Damburneya maritima Raf., Sylva Tellur. 136 (1838), nom. illeg., based on *Laurus catesbyana* Michx., Fl. Bor.-Amer. 1: 244 (1803).

Damburneya was recently reinstated (Trofimov *et al.*, 2016), because the species treated as belonging to the *Nectandra coriacea* group (Rohwer, 1993b) do not form a monophyletic group with the main part of the genus *Nectandra*. In addition to the species recognized by Trofimov *et al.* (2016), we transfer four additional species to *Damburneya* here.

The species hitherto known as *Nectandra earlei* Britton ex Roig & Acuña (nom. illeg.) or *N. minima* Rohwer already had been treated as a member of the *N. coriacea* group (Rohwer, 1993b), but was not transferred to *Damburneya* in our previous paper because it is morphologically somewhat aberrant and we did not have molecular data at that time. Now the DNA sequences confirm that it is a species of *Damburneya*. The reasons for transferring the three species previously recognized as *Aiouea guatemalensis*, *A. inconspicua* and *A. parvissima* have been described above. As a consequence, the diagnosis of *Damburneya* as given in Trofimov *et al.* (2016) needs to be broadened to include species with disporangiate as well as tetrasporangiate anthers.

1. *Damburneya guatemalensis* (Lundell) Rohwer, comb. nov.

≡ *Aniba guatemalensis* Lundell, Wrightia 4: 98–99 (1969) [basionym]

≡ *Aiouea guatemalensis* (Lundell) S.S. Renner, Fl. Neotrop. Monogr. 31: 93 (1982).

Type: Guatemala: Alta Verapaz: Chahal, 6.5 km on El Mago, bordering Sebol Road, 15 Oct 1968, *Contreras* 7941; *holotype:* LL00031105 [photograph]; *isotypes:* LL00370845 [photograph], MO-247056!, MSC0129892 [photograph], S Number S-R-7255 [photograph].

2. *Damburneya inconspicua* (van der Werff) Trofimov, comb. nov.

≡ *Aiouea inconspicua* van der Werff, Ann. Missouri Bot. Gard. 74: 401 (1987) [basionym]

Type: Mexico. Veracruz: 0–2 km S del campamento Hnos. Cedillo, rumbo a Río Alegre, por la desviación al E, Hidalgotitlán, alt. 140 m, 22 Apr 1974, *Brigada Dorantes* 2929; *holotype:* MO-247055; *isotypes:* C10013488 [photograph], MO-247054, BM000993899 [photograph], BM000993900 [photograph], UC1439911, XAL0106595.

3. *Damburneya minima* (Rohwer) Trofimov, comb. nov.

≡ *Nectandra minima* Rohwer, Fl. Neotrop. Monogr. 60: 57 (1993) [basionym]

Type: Cuba. Isla de la Juventud: near Nueva Gerona, 04 Jun 1904 (fl), *Curtiss* 526; *holotype:* F0061473F!; *isotypes:* A00273103!, BM000758718!, G00369038!, GH00273104!, HBG-509919!, L1802391!, M!, MO-277522!, NY!.

= *Nectandra earlei* Britton ex Roig & Acuña, Revista Soc. Cub. Bot. 6: 17 (1949), nom. illeg., excl. synon.

4. *Damburneya parvissima* (Lundell) Trofimov, comb. nov.

≡ *Aniba parvissima* Lundell, Wrightia 4: 31 (1969) [basionym]

≡ *Aiouea parvissima* (Lundell) S.S. Renner, Fl. Neotrop. Monogr. 31: 98 (1982).

Type: Guatemala. Petén: La Cumbre (fl), 23 Sep 1966, *Contreras* 6204; *holotype:* LL00031103 [photograph]; *isotypes:* F0061335F [photograph], K000601920 [photograph], K000601921 [photograph], LL00031104 [photograph], MO-247052!, NY [photograph].

II. *Mespilodaphne* Nees & Mart. in Nees, Linnaea 8: 45 (1833).

Type: Mespilodaphne pretiosa Nees & Mart. in Nees, Linnaea 8: 45 (1833).

= *Dendrodaphne* Beurl., Kongl. Vetensk.-Akad. Handl. 1854: 145 (1856).

≡ *Ocotea* subgenus *Dendrodaphne* Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 236 (1889).

Type: Dendrodaphne macrophylla Beurl., Kongl. Vetensk.-Akad. Handl. 1854: 145 (1856).

= *Sassafridium* Meisn., Prodr. [A. P. de Candolle] 15(1): 171 (1864).

Type: Sassafridium veraguense Meisn., Prodr. [A.P. de Candolle] 15(1): 171 (1864).

Diagnosis: Leaves glabrous or nearly so; inflorescences in the axils of bracts near the tips of the twigs; flowers relatively large, with spreading tepals; stamens tongue-shaped (Fig. 6A, B), heavily papillose, with four locules in two pairs, one above the other, latrorse in the third whorl; staminodes usually present but inconspicuous, conical, papillose; cupule distinctly double-rimmed (similar to Fig. 4C), with spreading outer margin.

Description: Trees or shrubs; leaves evergreen, alternate, lanceolate to elliptic, glabrous or very sparsely pubescent; inflorescences in the axils of cataphylls immediately below the terminal vegetative bud, few-flowered, with up to two orders of branching; flowers trimerous, bisexual, tepals six, stamens nine, all tongue-shaped and heavily papillose; staminodes usually present but inconspicuous, conical, papillose, squeezed in between the bases of the stamens of the third whorl; ovary inserted in a relatively deep, hemispherical to almost urceolate receptacle; cupule distinctly double-rimmed, with spreading outer margin.

Etymology: The name *Mespilodaphne* was coined by Nees & Martius (in Nees, 1833), who included three species in this genus, *Mespilodaphne pretiosa* Nees & Mart., *M. leucophloea* Nees & Mart., and *M. prolifera* Nees & Mart. In the latter two, they added a question mark behind the genus name, so that it is clear that *M. pretiosa* should be the type species. As Nees & Martius cited the earlier name *Laurus quixos* Lam. in synonymy, the species name *M. pretiosa* is illegitimate, but nevertheless the genus *Mespilodaphne* is legitimate. It is typified by the type of the species currently known as *Ocotea quixos* (Lam.)

Kosterm.: [Ecuador] 'ex Provincia de los Canelos in Peru', 1748, *Joseph de Jussieu s.n.* (P00307277!). The specific epithet refers to the Quijos valley, east of Quito in the province of Napo (Naranjo *et al.*, 1981). A label on the specimen says that Jussieu described the species in a letter sent from a place in the province of Riobamba (now prov. Chimborazo) on 12 April 1748. Thus, the actual date of collection probably was earlier. For further details, also on the other elements included in *M. pretiosa*, see Moraes (2008). The name *Mespilodaphne* means 'medlar laurel'. It refers to material with immature fruits included in *M. pretiosa* var. *latifolia* Nees & Mart., currently treated as a synonym of *Ocotea odorifera* (Vell.) Rohwer, in which an almost spherical, lenticellate cupule includes a berry that is still so small it does not reach beyond the rim of the cupule, so the whole structure resembles the fruit of the common medlar, *Mespilus germanica* L. The fruit of *Mespilodaphne quixos*, however, is quite different, roughly acorn-like, with a conspicuously double-rimmed cupule in which the outer margin is spreading and the inner one is appressed to the berry. It is sold in the markets in Ecuador as a spice because of its strong cinnamon odor (Naranjo *et al.*, 1981).

Due to the obviously erroneous inclusion of *Laurus quixos* in the type species of *Mespilodaphne*, the name must now be applied to a group for which it was never intended by Nees (1833, 1836), nor by Meissner (1864). We therefore accept none of the 49 species recognized by Meissner (1864), nor any of those that have been added to this genus later.

Distribution and habitat: Species of *Mespilodaphne* occur in South America, Central America and the Antilles in tropical forests up to 2000 m elevation.

Observations: Mespilodaphne is most easily recognized by its heavily papillose, tongue-shaped stamens. In contrast to *Nectandra*, in which similarly papillose stamens are found in several species, it has retained the plesiomorphic position of the pollen sacs in two superposed pairs. A few species of the *Ocotea helicterifolia* group (*O. botrantha*, *O. sinuata*, *O. verticillata*) have similar stamens, but differ by a conspicuous, erect indument on leaves and twigs, whereas these parts are (sub)glabrous in *Mespilodaphne*. Another characteristic of this genus are the distinctly double-rimmed cupules in fruit. This seems to be a synapomorphy of a larger group, but at present our data do not allow to determine precisely when it arose (see above). In the analysis of Chanderbali *et al.* (2001) it seemed that clearly double-rimmed cupules had arisen only once, in one of the two branches of their '*Licaria* group and allies', but their analysis included only a single member of the *Ocotea indecora* group, *O. odorifera*.

Mespilodaphne includes the following species:

1. ***Mespilodaphne cymbarum*** (Kunth) Trofimov, comb. nov.

≡ *Ocotea cymbarum* Kunth in Humbold, Bonpland and Kunth, Nov. Gen. Sp. 2: 132–133 [folio ed.] or 166–167 [quarto ed.] (1817) [basionym]

≡ *Nectandra cymbarum* (Kunth) Nees, Syst. Laurin. 305 (1836).

≡ *Licaria cymbarum* (Kunth) Pittier, Bol. Soc. Venez. Ci. Nat. 7: 135 (1941).

≡ *Misanteca cymbarum* (Kunth) Lundell, Wrightia 4: 100 (1969).

Type: Venezuela. Amazonas: 'In sylvis Orinocensibus prope San Fernando de Atabapo', May, fr., *Humboldt & Bonpland* 904; *lectotype:* B-W 07787010! (designated by Moraes, 2013) [Mus. Bot. Berol. Film Nr. 657/28]; *isotype:* P00128760!.

= *Ocotea amara* Mart. in Buchner, Repert. 35: 180 (1830).

Type: Brazil. Amazonas: 'In sylvis aboriginibus Provinciae Fluminis nigri', 1820, fr., *Martius s.n.*; *holotype:* M-0147301!; *isotypes:* B 10 0185242!, L0036963!; fragm. GZU000254306!.

= *Nectandra barcellensis* Meisn., Prodr. [A.P. de Candolle] 15(1): 155 (1864).

≡ *Ocotea barcellensis* (Meisn.) Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 237 (1889).

Type: Brazil. Amazonas: between Barcellos and San Isabel, Dec 1851, *Spruce* 1925; *lectotype:* G00131425! (designated by Rohwer, 1986, as 'Holotyp'); *isotypes:* AWH number 28256, B 10 0185281! [F neg. 3628], BM001009300!, BR0000008813558!, E00259368! [photograph], G00369375!, G00369376!, GH00042080, GOET004532!, K000602177!, K000602245!, LD acc. number 1517272 [photograph], LE00000224!, MG019408!, NY00355421!, OXF!, P00711159!, P00711160!.

= *Nectandra caparrapi* Sand.-Groot ex Nates, Aceite Amacey también llamado Aceite de Caparrapí 13, 15, 43 (1889).

≡ *Nectandra oleifera* Posada-Ar. ex Nates, ibid., 43 (1889).

≡ *Oreodaphne oleifera* Posada-Ar., Revista Médica de Bogotá (1890).

≡ *Ocotea caparrapi* (Nates) Dugand, Rev. Acad. Colomb. 3: 396 (1940).

Type: Colombia. Cundinamarca: Mun. Caparrapí, Hacienda Saldaña, alt. 1280 m, 10–13 Jun 1939, *Garcia Barriga* 7661; *neotype:* COL000001389 [photograph] (designated by Dugand, 1940); *isotypes:* COL000001390 [photograph]; fragm. G!, HBG!.

= *Nectandra elaiophora* Barb. Rodr., Vellosia, ed. 2, 1: 64–66 (1891).

Type: Brazil. Amazonas: Ad ripas Rio Negro, *Barbosa Rodriques, Museu Botanico do Amazonas* 646 (missing, most likely destroyed); *lectotype:* [icon] tab. XVIII in Vellosia, ed. 2, vol. 3. 1891 (here designated).

Observations: The holotype of *Nectandra elaiophora* has not been cited as seen by any subsequent author and may have been lost. If that was the case, then the collection cited by Ducke (1930) might serve as neotype: Brazil, Amazonas: Manaus, Paraná do Careiro, 12 Jun 1927, *Ducke s.n.*, RB19936 (G!, K!, NY00355433!, P!, RB number 19936!, S!). According to Dugand (1940), no type was cited in the original description of *N. caparrapi*.

2. *Mespilodaphne fragrantissima* (Ducke) Trofimov, comb. nov.

≡ *Ocotea fragrantissima* Ducke, Trop. Woods 60: 7–9 (1939) [basionym]

Type: Brazil. Amazonas: near the lower Rio Curicuriari, a tributary of Rio Negro, 04 Oct 1935, *Ducke s.n.*, RB35184; *lectotype:* RB00539224! (here designated); *isotypes:* B 10 0185335!, B 10 0185336!, G00369422! (mounted on two sheets), K000602399!, NY00162367!, NY00162368!, NY00162369!, P00756882!, P00756883!, RB00545247!, S-R-7152, U0002946 [photograph], US00051066!.

3. ***Mespilodaphne klepperae*** (van der Werff) Trofimov, comb. nov.

≡ *Ocotea klepperae* van der Werff, Novon 11: 508 (2001) [basionym]

Type: Costa Rica. Puntarenas: Parrita, valley of Río Palo Seco, base of Cerro Cabeza de Chancho, 09°36’44”N, 084°14’00”W, 330 m, 21 Feb 2000, *Hammel* 22068; *holotype:* INB; *isotypes:* MO-247518 [photograph], MO-247519 [photograph].

4. *Mespilodaphne macrophylla* (Beurl.) Trofimov, comb. nov.

≡ *Dendrodaphne macrophylla* Beurl., Kongl. Vetensk.-Akad. Handl. 1854: 145 (1856) [basionym]

≡ *Ocotea dendrodaphne* Mez, Jahrb. Königl. Bot. Gart Berlin 5: 238 (1889).

Type: Panama. Colón: Portobelo, Apr 1826, *Billberg s.n.*; *holotype:* S-R-7245!.

= *Ocotea quisara* Mez & Donn.Sm., Bot. Gaz. (Crawfordsville) 33: 259 (1902).

Type: Costa Rica. Cartago: Atirro, alt. 600 m, Apr 1896, *Donnell Smith* 6753; *lectotype:* US00997607 (here designated); *isotype:* K000602163!.

= *Ocotea ovandensis* Lundell, Contr. Univ. Michigan Herb. 6: 16–17 (1941).

Type: Mexico. Chiapas: Mt. Ovando, 17 Dec 1936, *Matuda* 444; *holotype:* MICH1104596 [photograph]; *isotypes:* CAS0003651 [photograph], F0075496F!, LL00370918 [photograph], NY00355558!, US00099236!.

Observations: Not many of the syntypes of *Ocotea quisara* have been annotated by Mez. Among these, we selected the most complete flowering specimen as lectotype. The other syntypes are: Costa Rica, Alajuela: Llanuras de Santa Clara, La Emilia, alt. 250 m, Apr 1896, *Donnell Smith* 6751 (B 10 0244365!, GH00042052 [photograph], K000602164! [on the same sheet as K000602165], US00997606!; fragm. B 10 0244364!); Costa Rica, Alajuela: Llanuras de Santa Clara, La Concepción, alt. 250 m, Feb 1896, *Donnell Smith* 6756 (BM!, GH00042053 [photograph], K000602165! [on the same sheet as K000602164], US00048359!, US00997605 [photograph]).

5. *Mespilodaphne morae* (Gómez-Laurito) Trofimov, comb. nov.

≡ *Ocotea morae* Gómez-Laurito, Novon 7: 145–146 (1997) [basionym]

Type: Costa Rica. Alajuela: San Ramón, Reserva Biológica Alberto M. Brenes, 10°13’N, 84°37’W, alt. 800–850 m, 27 Aug 1995, *Gómez-Laurito & Mora* 12817; *holotype:* USJ; *isotypes:* CR, F, MO-247511 [photograph].

6. *Mespilodaphne quixos* (Lam.) Rohwer, comb. nov.

≡ *Laurus quixos* Lam., Encycl. Méth. Bot. 3: 455 (1792) [basionym]

≡ *Mespilodaphne pretiosa* Nees & Mart. in Nees, Linnaea 8: 45 (1833), nom.illeg.

≡ *Ocotea quixos* (Lam.) Kosterm., Recueil Trav. Bot. Néerl. 35: 900 (1938).

≡ *Licaria quixos* (Lam.) Kosterm., Reinwardtia 7: 146 (1965).

≡ *Misanteca quixos* (Lam.) Lundell, Wrightia 4: 101 (1969).

Type: Ecuador. ‘Prov. de los Canelos’: 12 Apr 1748, *Herb. de Jussieu s.n.*; *holotype:* P00307277!; *isotype:* P00381527! [‘prov. Riobamba’]; possible type fragment, G00369326!.

= *Laurus cinnamomoides* Kunth, Nov. Gen. Sp. 2: 134 [folio ed.] or 169 [quarto ed.] (1817).

≡ *Nectandra cinnamomoides* (Kunth) Nees, Syst. Laurin. 307 (1836).

≡ *Acrodiclidium cinnamomoides* (Kunth) Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 88 (1889).

≡ *Ocotea cinnamomoides* (Kunth) Kosterm., J. Sci. Res. (Jakarta) 1: 116 (1952), nom.illeg., non Scheidweiler, Hort. Belge 4: 364 (1837).

Type: Colombia. Tolima: near Mariquita, alt. 900 m, Jun 1801, *Humboldt & Bonpland* 1722; *lectotype:* P00128749! (here designated); *isotypes:* B-W

7770 = two specimens, B-W 07770-01 0 and B-W 07770-02 0 [F neg. 3839], HAL0010369, NY00355160!, P00128750!, P00128751!, P00128763!.

7. *Mespilodaphne staminea* (Griseb.) Trofimov, comb. nov.

≡ *Nectandra staminea* Griseb., Fl. Brit. W. I.: 282–283 (1860) [basionym]

≡ *Synandrodaphne antillana* Meisn., Prodr. [A.P. de Candolle] 15(1): 176 (1864), nom. illeg.

≡ *Ocotea staminea* (Griseb.) Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 240 (1889).

Type: Jamaica. St. Ann: between Green Park and Brown's Town, 26 Jul 1850, *Alexander s.n.*; *lectotype:* GOET004553! (here designated); *isotypes:* B 10 0086074!, K000602127! [collector not indicated, from heritage of Prior, but with the same label data], P00711096!; fragm. NY00074365!.

= *Oreodaphne fragrans* Meisn., Prodr. [A.P. de Candolle] 15(1): 127 (1864).

Type: Jamaica. Westmoreland: [locality illegible], Feb 1844, *Purdie s.n.*; *holotype:* K000602124!; *isotypes:* K000602123!, K000602126!, K000602128!.

Observations: The specimen GOET004553 was selected as lectotype of *Nectandra staminea* because it is the best flowering specimen bearing Grisebach's handwriting. We found the following additional syntypes: Jamaica, St. Ann: *McNab s.n.* (GOET004552!). Jamaica, Westmoreland: [locality illegible], Feb 1844, *Purdie s.n.* (K000602123!, K000602124!, K000602126!, K000602128!). The last syntype is the type of *Oreodaphne fragrans* Meisn. The specimen K000602125, annotated by Grisebach and therefore labelled as a syntype of *Nectandra staminea* by the senior author in 1983, apparently has been collected by William Thomas March, and thus is not a type.

8. *Mespilodaphne veraguensis* (Meisn.) Rohwer, comb. nov.

≡ *Sassafridium veraguense* Meisn., Prodr. [A.P. de Candolle] 15(1): 171 (1864) [basionym]

≡ *Ocotea veraguensis* (Meisn.) Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 240 (1889).

Type: Panama, Veraguas: 1855, *Bridges s.n.*; *lectotype:* K000602162! (here designated).

= *Ocotea paradoxa* Mez, Bot. Jahrb. 30, Beibl. 67: 16–17 (1901).

Type: Costa Rica. Guanacaste: Río Naranjo, alt. 200–300 m, Mar 1893, *Tonduz* 7648; *holotype:* BR0000005119 69!; *isotype:* B 10 0243852!.

= *Ocotea bakeri* Blake, Contr. Gray Herb. 52: 65–66 (1917).

Type: Nicaragua. Volcán Mombacho: alt. 600–1100 m, 20 Feb 1903, *Baker* 2493; *holotype:* GH00042032!; *isotypes:* BM000990031!, CAS0003645, CAS0213919 [photograph], CM0646 [photograph], F0061538F!, GH00042031 [photograph], MICH1104588 [photograph], MO-247484!, MSC0092472 [photograph], NY00355552!, OKLA100131 [photograph], PH00019558 [photograph], PH00019559 [photograph], RSA0004132 [photograph], UC986711, US00099203!, WISv0255267WIS [photograph].

= *Ocotea escuintlensis* Lundell, Contr. Univ. Michigan Herb. 6: 15–16 (1941).

Type: Mexico. Chiapas: Escuintla, 03 May 1936, *Matuda* 654; *holotype:* MICH1210267 [photograph]; *isotypes:* CAS0003646 [photograph], LL00370908 [photograph], US00048575!; fragm. A00042037 [photograph].

Observation: We know of only two additional syntypes of *Sassafridium veraguense*: 'in monte aguacate', *Oersted* Laur. 10 (B 10 0243818!); 'Costa Rica et Veragua', *Warszewicz* 1 (G00369081!).

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APPENDIX. SPECIES EXAMINED. TAXON, ORIGIN, VOUCHER INFORMATION AND GENBANK/NCBI ACCESSION NUMBERS.

Species transferred to another genus at the end of the paper are listed under their new name, with the previous name in parentheses.

Accession numbers beginning with AF2 are from Chanderbali *et al.* (2001); with AF3 from Chanderbali (2004); with EU from Madriñán & Chacón (unpubl.); with GQ4 from Assis & Mello-Silva (unpubl.); with GQ9 from Kress *et al.* (2005); with FM from Rohwer *et al.* (2009); with KF from Bolson *et al.* (2015); with KX from Trofimov *et al.* (2016); with MF from Rohde *et al.* (2017). Numbers beginning with MK are new sequences. The first number is the sequence of the nuclear ITS sequence and the second number the plastid *psbA-trnH* spacer.

'Aiouea' costaricensis (Mez) Kosterm., Costa Rica, Heredia, 03 Apr 1987, *Grayum 8241* (HBG), MF110010, MF137930;

'Aiouea' obscura van der Werff, Costa Rica, Puntarenas, 16 Mar 2017, *Aguilar 016017* (MO), MK507230, MK507298;

'Aiouea' vexatrix van der Werff, Panama, Panamá, 10 Sep 1970, *Croat 12153* (HBG), MF110033, MF137953;

Aniba affinis (Meisn.) Mez, Brazil, Amazonas, 06 Mar 1989, *Ziburski 89/7* (HBG), MK507231, MK507299;

A. firmula (Nees & Mart.) Mez, Brazil, São Paulo, 01 Sep 2011, *Moraes 3356* (HRCB), MF110034, MF137954;

A. taubertiana Mez, Peru, Madre de Dios, 24 Nov 2002, *Valenzuela 1028* (HBG), MK507233, MK507301;

Damburneya ambigens (S.F.Blake) Trofimov, Mexico, Veracruz-Oaxaca, 15 Apr 1981, *Wendt 3190* (HBG), KX509828, KX509888;

D. colorata (Lundell) Trofimov, Mexico, Oaxaca, 26 Sep 1986, *Hammel 15466* (HBG), MK507234, MK507302;

D. coriacea (Sw.) Trofimov & Rohwer, USA, Fairchild Trop. Gard., 08 Oct 1997, *Zona s.n.* (HBG), KX509829, KX509889;

D. gentlei (Lundell) Trofimov, Mexico, Veracruz-Oaxaca, 25 Mar 1981, *Wendt 3060* (HBG), KX509830, KX509890;

D. *(Aiouea)* ***guatemalensis*** (Lundell) Rohwer, Guatemala, Izabal, 10 Sep 1970, *Contreras 10251* (HBG), MF110015, MF137935;

D. *(Aiouea)* ***inconspicua*** (van der Werff) Trofimov, Mexico, Veracruz, 20 Jan 1985, *Ibarra-Manríquez 2236* (HBG), MK507235, MK507303;

D. martinicensis (Mez) Trofimov, Belize, Cayo, 04 Jul 2006, *Vandrot 123* (HBG), KX509831, KX509891;

D. *(Nectandra)* ***minima*** (Rohwer) Trofimov, Cuba, Isla de la Juventud, 06 Nov 1981, *Álvarez de Zayas 45785* (JE), MK507236, MK507304;

D. *(Aiouea)* ***parvissima*** (Lundell) Trofimov, Guatemala, Petén, 19 Feb 1975, *Lundell 19008* (HBG), MK507237, MK507305;

D. patens (Sw.) Trofimov, Jamaica, Surrey, 06 Nov 1980, *Kapos 1584* (HBG), KX509832, KX509892;

D. purpurea (Ruiz & Pav.) Trofimov, **#1:** Peru, Cajamarca, 18 Dec 1996, *Campos 3165* (MO), AF272293, —; **#2:** Panama, Panamá, date not indicated, *BCI 415163* (ANDES), —, EU153974;

D. salicifolia (Kunth) Trofimov & Rohwer, **#1:** Costa Rica, *Gomez-Laurito s.n.* (–), AF272294, —; **#2:** Belize, without locality and date, *Baden 977*1* (HBG), —, KX509893;

D. smithii (C.K.Allen) Trofimov & Rohwer, Costa Rica, Puntarenas, 09 Aug 1987, *Haber 7478* (HBG), MK507238, MK507306;

D. umbrosa (Humboldt, Bonpland & Kunth) Trofimov, Costa Rica, Puntarenas, 23 Feb 1988, *Kernan 208* (HBG), MK507239, MK507307;

Dicypellium aphyllaceum (Mart.) Nees, Brazil, Pará, 27 Dec 1983, *Pires 16756* (HBG), MK507240, MK507308;

D. manausense W.A.Rodrigues, Brazil, Amazonas, 09 Dec 1997, *Assunção 749* (MO), AF272270, AF268775;

Endlicheria chalisea Chanderb., Peru, Pasco, 30 Jan 2008, *Rojas 5265* (HBG), MK507241, MK507309;

E. citriodora van der Werff, Peru, Loreto, 26 Jul 1988, *van der Werff 9776* (HBG), MK507242, MK507310;

E. longicaudata (Ducke) Kosterm., **#1:** Brazil, Amazonas, 14 Aug 1996, *Assunção 366* (MO), AF363375, —; **#2:** Brazil, Pará, 28 Aug 1979, *Cid 881* (HBG), —, MK507311;

E. punctulata (Mez) C.K.Allen, Suriname, Sipaliwini, 18 Apr 1998, *Hammel 21557* (HBG), MK507243, MK507312;

E. pyriformis (Nees) Mez, Guyana, U.Takutu-U.Essequibo, 31 Aug 1999, *H.D. Clarke 8070* (US), MK507244, MF137986;

Kubitzkia mezii (Kosterm.) van der Werff, Guyana, Potaro-Siparuni, 08 Jul 1997, *Chanderbali 249* (MO), AF272276, AF268772;

Licaria armeniaca (Nees) Kosterm., Peru, Loreto, 09–10 Aug 1994, *Kvist & Ruiz 1052* (AAU), MK507245, MK507314;

L. bahiana H.W.Kurz, Brazil, Espírito Santo, 06 Sep 2011, *Moraes 3166* (HRCB), MF110068, MF137988;

L. pachycarpa (Meisn.) Kosterm., Guyana, U.Takutu-U.Essequibo, 18 Sep 1993, *Henkel 3021* (HBG), MK507247, MK507316;

L. rodriguesii H.W.Kurz, Brazil, Pará, 14 May 1969, *Silva 1960* (HBG), MK507248, MK507317;

Mespilodaphne** (Ocotea)* ***cymbarum (Kunth) Trofimov, Brazil, Amazonas, 28 Sep 1975, *Kubitzki 75–99* (HBG), MK507249, MK507318;

M.** (Ocotea)* ***quixos (Lam.) Rohwer, Ecuador, Napo, 23 Nov 1990, *Neill 9487* (MO), MF110080, KX509937;

Machilus grijsii Hance, Germany, Hamburg Bot. Gard., 23 Jan 2013, *Rohwer 193* (HBG), KX509833, FM957810;

Nectandra angusta Rohwer, Bolivia, Tarija, 20 Feb 2006, *Zenteno 3903* (HBG), KX509835, KX509896;

N. apiculata Rohwer, Bolivia, Santa Cruz, 24 Mar 1981, *Beck 6806* (HBG), KX509836, KX509897;

N. barbellata Coe-Teix., Brazil, São Paulo, 24 Aug 2011, *Moraes s.n.* (HRCB), KX509837, KX509898;

N. citrifolia Mez & Rusby, Ecuador, Esmeraldas, 12 Feb 1996, *Clark 2065* (HBG), KX509842, KX509902;

N. cuspidata Nees & Mart. ex Nees, **#1:** locality and date not indicated, *Assis 1151* (herbarium not indicated), GQ480369, —; **#2:** locality and date not indicated, *FC 1579* (ANDES), —, EU153966;

N. grandiflora Nees, Brazil, São Paulo, 03 Jun 2011, *Moraes 3148* (HBG), KX509845, KX509905;

N. hihua (Ruiz & Pav.) Rohwer, Cuba, Holguín, 03 May 1980, *Álvarez de Zayas 42637* (JE), KX509847, KX509907;

N.* cf. *lineata (Kunth) Rohwer, Peru, Amazonas, 01 Nov 2012, *van der Werff 24827* (HBG), KX509839, —;

N. lineata (Kunth) Rohwer, Panama, Panamá, date not indicated, *Perez 441778* (STRI), —, GQ982298;

N. lineatifolia (Ruiz & Pav.) Mez, Bolivia, La Paz, 07 Aug 2003, *Beck 28963* (HBG), KX509851, KX509912;

N. longifolia (Ruiz & Pav.) Mez, Bolivia, La Paz, 25 Sep 1991, *Seidel 5346* (HBG), KX509852, KX509913;

N.* cf. *matthewsii Meisn., Peru, Pasco, 13 Aug 2003, *Rojas 1262* (HBG), KX509840, KX509900;

N. maynensis Mez, Peru, Pasco, 21 Jul 2006, *Monteagudo 12454* (HBG), KX509853, KX509914;

N. membranacea (Sw.) Griseb., Brazil, Espírito Santo, 19 Jan 1995, *Moraes 1157* (HRCB), KX509854, KX509915;

N. micranthera Rohwer, Brazil, Bahia, 02 Mar 1978, *Mori 9358* (HBG), KX509855, KX509916;

N. olida Rohwer, Peru, Amazonas, 05 Nov 2012, *van der Werff 25083* (HBG), KX509859, KX509920;

N. turbacensis (Kunth) Nees, **#1:** Puerto Rico, Río Grande, 25 May 1994, *Taylor 11746* (MO), AF272295, —; **#2:** Panama, Panamá, date not indicated, *BCI 415163* (ANDES), —, EU153974;

Ocotea aciphylla (Nees) Mez, **#1:** Brazil, Espírito Santo, 09 Sep 2011, *Moraes 3210* (HRCB), KX509866, —; **#2:** Brazil, Espírito Santo, 09 Sep 2011, *Moraes 3205* (HRCB), —, KX509929;

O. arcuata Rohwer, Panama, Panama, 26 Jan 1986, *McPherson & Merello 8145* (HBG), MK507250, MK507319;

O. atirrensis Mez & Donn.Sm., Costa Rica, Limón, 28 Aug 1991, *Jiménez 1014* (HBG), MF110071, MF137995;

O. aurantiodora (Ruiz & Pav.) Mez, Bolivia, La Paz, 09 Jul 2005, *Beck 30448* (HBG), MK507251, MK507320;

O. balanocarpa (Ruiz & Pav.) Mez, Peru, Cusco, 23 Nov 2006, *Valenzuela 8092* (HBG), MK507252, MK507321;

O. botrantha Rohwer, Guatemala, Quetzaltenango, 21 Apr 2013, *Wernisch s.n.* (HBG), KX509867, KX509930;

O. brenesii Standl., Costa Rica, Alajuela, 19 Mar 1985, *Haber 1559* (HBG), MK507253, MK507322;

O. bullata (Burch.) E.Mey., South Africa, Natal, 23 Jan 1994, *Abbot 6208* (MO), AF267778, AF272298;

O. caniflora Mez, Peru, Cusco, 14 May 2005, *Calatayud 3046* (HBG), MK507254, MK507323;

O. catharinensis Mez, Brazil, Espírito Santo, 10 Sep 2011, *Moraes 3232* (HRCB), MK507255, MK507324;

O. complicata (Meisn.) Mez, Brazil, Bahia, 11 Nov 2009, *Moraes 2999* (HBG), MK507256, MK507325;

O. congregata van der Werff, Mexico, Chiapas, 15 Oct 1985, *Méndez 8503* (HBG), MK507257, MK507326;

O. cujumary Mart., Guyana, Upper Takutu-Upper Essequibo, 10 Sep 1999, *H.D. Clarke 8384* (US), MK507258, MK507327;

O. daphnifolia (Meisn.) Mez, Brazil, Espírito Santo, 11 Sep 2011, *Moraes 3239* (HRCB), MK507259, MK507328;

O. dentata van der Werff, Costa Rica, Limón, 23 Oct 1994, *Gómez-Laurito 12754* (HBG), MK507260, MK507329;

O. divaricata (Nees) Mez, Brazil, Espírito Santo, 06 Sep 2011, *Moraes 3185* (HRCB), MK507261, MK507330;

O. domatiata Mez, Brazil, Espírito Santo, 11 Sep 2011, *Moraes 3237* (HRCB), MK507262, MK507331;

O. fasciculata (Nees) Mez, Guyana, Upper Takutu-Upper Essequibo, 31 Aug 1999, *H.D. Clarke 8099* (US), MK507263, MK507332;

O. floccifera Mez & Sodiro, Ecuador, Esmeraldas, 20 Aug 1989, *Palacios 4370* (HBG), MF110074, MF137998;

O. glaucosericea Rohwer, Ecuador, Imbabura, 11–14 Aug 1990, *Rubio & Quetal 593* (HBG), MK507264, MK507333;

O. glaziovii Mez, Brazil, Espírito Santo, 08 Sep 2011, *Moraes 3197* (HRCB), MK507265, MK507334;

O. guatemalensis Lundell, Guatemala, Baja Verapaz, 03 Dec 1976, *Lundell 20431* (HBG), MK507266, MK507335;

O. guianensis Aubl., Guyana, Upper Demerara-Berbice, 03 June 1997, *Chanderbali 232* (MO), AF268762, AF272302;

O. helicterifolia (Meisn.) Hemsl., Mexico, Oaxaca, 21 Feb 1988, *Campos 1328* (HBG), AF272303, MK507336;

O. holdridgeiana W.C.Burger, Costa Rica, Alajuela, 12 Jul 1991, *Jiménez 985* (HBG), MK507267, MK507337;

O. indecora (Schott) Mez, Brazil, Espírito Santo, 18 Dec 2012, *Moraes 3548* (HRCB), MF110076, MF138001;

O. insularis (Meisn.) Mez, Peru, Amazonas, 02 Feb 1995, *Rodríguez 329* (HBG), MK507269, MK507339;

O. javitensis (Kunth) Pittier, Ecuador, Napo, 08–17 Jan 1989, *Alvarado 245* (HBG), MK507270, MK507340;

O.* cf. *keriana A.C.Sm., Peru, Loreto, 09 Sep 1972, *Croat 20035* (HBG), MK507271, MK507341;

O. laetevirens Standl. & Steyerm., Mexico, Oaxaca, 26 Mar 1981, *Wendt 3074* (HBG), MK507272, MK507342;

O.* cf. *lancifolia (Schott) Mez, Brazil, Espírito Santo, 12 Sep 2011, *Moraes 3257* (HRCB), KX509868, KX509931;

O. laxa (Nees) Mez, Brazil, São Paulo, 17 Sep 2011, *Moraes s.n.* (HRCB), MK507273, MK507343;

O. lentii W.C.Burger, Costa Rica, Cartago, 22 Aug 1971, *Lent 2070* (HBG), MK507274, MK507344;

O. leptobotra (Ruiz & Pav.) Mez, **#1:** Peru, Madre de Dios, 20 Oct 2004, *Valenzuela 4225* (HBG), MK507275, —; **#2:** Panama, Panamá, date not indicated, *BCI 215988* (ANDES) —, EU153980;

O. macrophylla Kunth, Ecuador, Carchi, 30 Jul 1989, *van der Werff 10772* (HBG), KX509870, KX509932;

O. meziana C.K.Allen, Costa Rica, Puntarenas, 14 Dec 1985, *Bello 3833* (HBG), MK507276, MK507345;

O. micans Mez, Colombia, Antioquia, 12 Jan 2015, *Velez & Penagos 5275* (MEDEL), MK507277, MK507346;

O. minarum (Nees & Mart.) Mez, Brazil, Federal District, 12 May 1983, *Pereira 511* (HBG), MK507278, MK507347;

O. montana (Meisn.) Mez, Brazil, Bahia, 24 Oct 1988, *Folli 791* (HBG), MK507279, MK507348;

O. nitida (Meisn.) Rohwer, **#1:** locality and date not indicated, *Mello-Silva 2755* (herbarium not indicated), GQ480387, —; **#2:** Brazil, Espírito Santo, 12 Sep 2011, *Moraes 3256* (HRCB), —, MK507349;

O. oblonga (Meisn.) Mez, Costa Rica, Limón, 25 Jul 1989, *Herrera 3342* (HBG), MK507280, MK507350;

O. odorifera (Vell.) Rohwer, Brazil, São Paulo, date not indicated, *Moraes s.n.* (HRCB), KX509871, KX309930;

O. pauciflora (Nees) Mez, **#1:** Brazil, Pará, 18 Jul 1980, *Cid 1649* (HBG), MK507281, —; **#2:** Guyana, Demerara, 30 May 1997, *Chanderbali 219* (MO), —, AF268764;

O. percoriacea Kosterm., **#1:** Brazil, Minas Gerais, 21 Jan 1995, *Lorea-Hernández 5584* (MO), AF272311, —; **#2:** Brazil, Minas Gerais, 14 Oct 2012, *Moraes 3503* (HRCB), —, MK507351;

O. pomaderroides (Meisn.) Mez, **#1**: locality and date not indicated, *Mello-Silva 2685* (herbarium not indicated), GQ480390, —; **#2:** Brazil, Bahia, 12 Dec 2009, *Moraes 3019* (HBG), —, MK507352;

O. porosa (Nees & Mart.) Barroso, Brazil, São Paulo, 29 Sep 2011, *Moraes 3375* (HRCB), MK507282, MK507353;

O. praetermissa van der Werff, Costa Rica, Cartago, 07 Mar 1987, *W.C. Burger 12065* (HBG), KX509872, KX509934;

O. puberula (Rich.) Nees, Brazil, Paraná, date not indicated, *Blum 10–069* (UPCB), KF420955, KF421042;

O. pulchella (Nees & Mart.) Mez, Brazil, São Paulo, 28 Aug 2011, *Moraes 3154* (HRCB), KX509873, KX509935;

O. purpurea (Mez) van der Werff, Guatemala, Baja Verapaz, 21 Jun 1977, *Lundell 21170* (HBG), KX509874, KX509936;

O. racemosa (Danguy) Kosterm., Madagascar, Toamasina, 16 May 1977, *Rakotomalaza 1325* (WAG), MK507283, MK507354;

O. rivularis Standl. & L.O.Williams, Costa Rica, Puntarenas, 08 Oct 1984, *Grayum 4069* (HBG), MK507284, MK507355;

O. salvadorensis (Lundell) van der Werff, El Salvador, Santa Ana, 25 Sep 1988, *Reyna 1414* (HBG), KX509875, KX509938;

O. sassafras (Meisn.) Mez, Brazil, Bahia, 22 Mar 2009, *Moraes 2605* (HBG), MK507285, MK507356;

O. sinuata (Mez) Rohwer, Costa Rica, San José, 08 Mar 1987, *W.C. Burger 12086* (HBG), KX509876, KX509939;

O. skutchii C.K.Allen, Costa Rica, Puntarenas, 20 Mar 1987, *W.C. Burger 12177* (HBG), MK507286, MK507357;

O. spectabilis (Meisn.) Mez, Brazil, Espírito Santo, 08 Sep 2011, *Moraes 3198* (HRCB), MK507287, MK507358;

O. teleiandra (Meisn.) Mez Brazil, São Paulo, 01 Sep 2011, *Moraes 3355* (HRCB), MK507288, MK507359;

O. tenera Mez & Donn.Sm., Costa Rica, Puntarenas, 15 Dec 1985, *Haber 3677* (HBG), MF110082, MF138006;

O. tessmannii O.Schmidt, Ecuador, Pastaza, 27 Feb–19 Mar 1985, *Neill 6093* (HBG), MK507290, MK507361;

O. usambarensis Engl., Kenya, Kieni, 26 Jun 1986, *Beentje 2915* (WAG), MK507291, MK507362;

O. valerioana (Standl.) W.C.Burger, Costa Rica, San José, 08 Mar 1987, *W.C. Burger 12097* (HBG), MK507292, MK507363;

Paraia bracteata Rohwer, H.G.Richt. & van der Werff, Brazil, Manaus, 30 Apr 1988, *Vicentini & van der Werff 1288* (MO), MK507293, MK507364;

Persea americana Mill., Germany, Hamburg Bot. Gard., 16 Oct 2003, *Rohwer s.n.* (HBG), KX509877, FM957821;

Phoebe sheareri (Hemsl.) Gamble, Germany, Hamburg Bot. Gard., 07 Jan 2014, *Rohwer s.n.* (HBG), KX509878, KX509940;

Pleurothyrium cuneifolium Nees, Peru, Pasco, 26 Nov 2009, *Valenzuela 13996* (HBG), KX509879, KX509941;

P. poeppigii Nees, Peru, Pasco, 23 Jun 2003, *van der Werff 17718* (HBG), KX509880, KX509942;

P. trianae (Mez) Rohwer, Peru, Pasco, 20 May 2009, *Rojas 6766* (HBG), MK507294, MK507365;

Rhodostemonodaphne negrensis Madriñán, Brazil, Amazonas, 30 Oct 1971, *Prance 15860* (HBG), MK507295, MK507366;

Rh. parvifolia Madriñán, Brazil, Amazonas, 01 Sep 1966, *Prance 2148* (HBG), AF363386, MK507367;

Umbellularia californica (Hook. & Arn.) Nutt., USA, Missouri Bot. Gard., 02 Oct 2000, *Chanderbali 326* (MO), AF272337, AF268777;

Urbanodendron bahiense (Meisn.) Rohwer, Brazil, São Paulo, 22 Jan 2013, *Moraes 3563* (HRCB), MK507296, MK507368;

U. verrucosum (Nees) Mez, Brazil, Espírito Santo, 12 Dec 2012, *Moraes 3531* (HRCB), MK507297, MK507369.

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