

# Phylogenetic study of the genus *Nectandra* (Lauraceae), and reinstatement of *Damburneya*

Dimitrij Trofimov, Barbara Rudolph & Jens G. Rohwer

Biozentrum Klein Flottbek und Botanischer Garten, Universität Hamburg, Ohnhorststr. 18, 22609 Hamburg, Germany

Author for correspondence: Jens G. Rohwer, [jens.rohwer@uni-hamburg.de](mailto:jens.rohwer@uni-hamburg.de)

ORCID JGR, <http://orcid.org/0000-0001-8560-9015>

DOI <http://dx.doi.org/10.12705/655.3>

**Abstract** Earlier studies indicated that the genus *Nectandra*, currently the second-largest genus of the Neotropical Lauraceae, might be diphyletic in its traditional circumscription, but the evidence was not quite conclusive. Our phylogenetic analyses based on nuclear (ITS) and chloroplast (*psbA-trnH*) sequences of 45 *Nectandra* species as well as 42 representatives of 18 genera of the core Lauraceae (*Ocotea* complex, Laureae, *Aiouea*, Asian *Cinnamomum* and *Persea* groups) confirm the suspicion that *Nectandra* is diphyletic. The two groups, *Nectandra* s.str. and the *N. coriacea* group, are each well supported in the maximum parsimony and Bayesian analyses, but they are not sister to each other. *Nectandra* s.str. is sister to *Pleurothyrium*, and the clade including *Nectandra* s.str. and *Pleurothyrium* is very likely closer to the dioecious taxa of the *Ocotea* complex. The *N. coriacea* group, on the other hand, appears to be closer to bisexual taxa known as the *Ocotea helicterifolia* group. In addition, *Nectandra* s.str. is characterized by a large deletion in the *psbA-trnH* spacer compared to all other core Lauraceae, including its sister group *Pleurothyrium*. Considering these facts, *Nectandra* cannot be maintained in the traditional sense. We therefore transfer the species of the *N. coriacea* group to the oldest generic name applied to this group, *Damburneya*. On the basis of fossil records from the American subcontinents and in accordance with previous phylogenetic and molecular clock studies we suggest a scenario of a climate-driven migration from North to South America, with a subsequent rapid radiation of *Nectandra* s.str. in South America.

**Keywords** *Damburneya*; ITS; Lauraceae; *Nectandra*; Neotropics; phylogeny; *psbA-trnH*

**Supplementary Material** Electronic Supplement (results of maximum parsimony analyses and Bayesian analyses of the individual markers) and the DNA sequence alignments are available in the Supplementary Data section of the online version of this article at <http://ingentaconnect.com/content/iapt/tax>

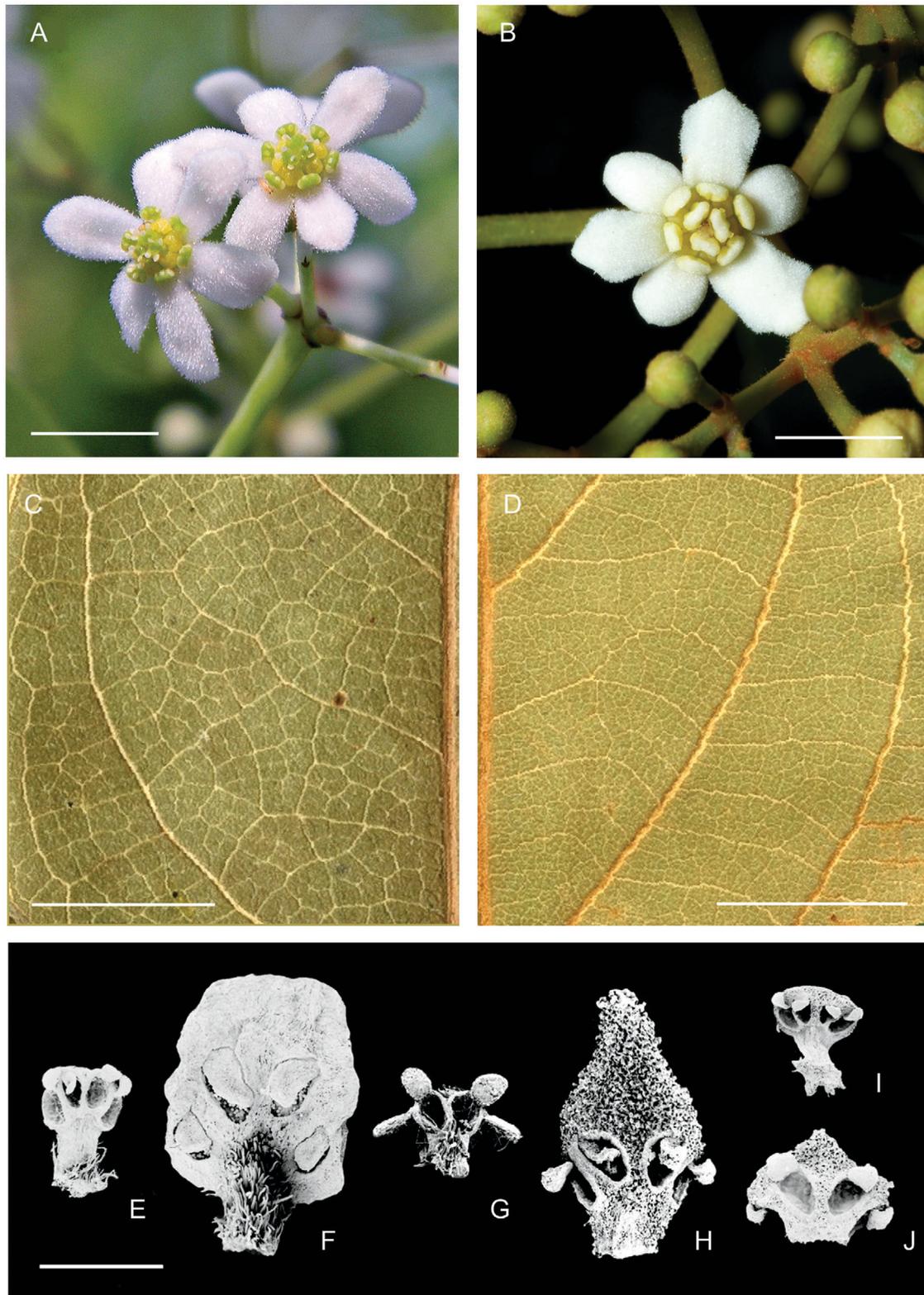
## ■ INTRODUCTION

*Nectandra* Rol. ex Rottb. is the second-largest genus of Lauraceae in tropical America, with 117 species currently recognized (Rohwer, 1993, 2012). It is distributed throughout the Neotropics, from Florida to Uruguay, with centers of diversity along the eastern slopes of the Andes and in southeastern Brazil. Species of *Nectandra* are found mostly in rainforests or at least seasonally moist forests from the lowlands to about 3000 m elevation. The genus is recognized by bisexual flowers (vs. unisexual in *Rhodostemonodaphne* Rohwer & Kubitzki), stamens with four pollen sacs arranged in a horizontal row or a relatively shallow arc (vs. two superposed pairs in several other genera), and by papillose, usually bright white tepals that are rotately spreading at anthesis and drop off as a ring together with the androecium afterwards (Van der Werff, 1991; Rohwer, 1993).

An explicit phylogenetic analysis of *Nectandra* has never been attempted, neither using morphological characters, nor DNA sequences. However, Rohwer designed a hypothetical scheme of the supposed relationships within the genus (Rohwer, 1993: fig. 10) based on morphology (mainly floral structures).

He assigned the species to thirteen groups based on flower structure, leaf venation and pubescence (Fig. 1). While most of these hypothetical groups were depicted as connected to several other groups, the *N. coriacea* group stands apart. Its species show those flower characters that are supposed to define *Nectandra*, but they also have characteristics of other genera of Lauraceae (Rohwer, 1993). Furthermore, the species of the *N. coriacea* group are distributed mainly in Central America and the Caribbean, whereas most of the other *Nectandra* species are distributed mainly in South America (Rohwer, 1993).

Also, a molecular phylogenetic study of the laurel family by Chanderbali & al. (2001) suggested a distinction between the *N. coriacea* group and the remaining *Nectandra* species. Their analysis of nuclear ribosomal internal transcribed spacer (ITS) sequences included three species of the *N. coriacea* group and four other species of *Nectandra*, and these two groups were separated by three nodes, one of them reasonably supported. *Umbellularia* (Nees) Nutt., the *Ocotea helicterifolia* group and *Pleurothyrium* Nees (in ascending order) appeared to be closer to the main part of *Nectandra* than the *N. coriacea* group. This of course raises the question



**Fig. 1.** **A & B,** Flowers of *Damburneya* (*N. coriacea* group) and *Nectandra* s.str.: **A,** *Damburneya coriacea* (*Nectandra coriacea*); **B,** *Nectandra barbellata*. **C & D,** Leaf venation patterns: **C,** *Damburneya coriacea* (*Nectandra coriacea*), with reticulate tertiary leaf venation; **D,** *Nectandra barbellata*, with scalariform tertiary venation. **E–J,** Stamen shapes in *Damburneya* and *Nectandra* s.str.: **E,** *Damburneya purpurea* (*Nectandra purpurea*) (Haber 1749); **F,** *Damburneya ambigens* (*Nectandra ambigens*) (Gentry 32253); **G,** *Damburneya coriacea* (*Nectandra coriacea*) (Lundell 19990); **H,** *Nectandra amazonum* (Kubitzki 79-69); **I,** *N. cuspidata* (Kubitzki 79-93); **J,** *N. hihua* (Van der Werff 10230). — Scale bars: A–D, 5 mm; E–J, 1 mm. Photographs by R. Peterson (A) and J.G. Rohwer (B–J).

if *Nectandra* is polyphyletic in its present circumscription. To answer this question, we examined 45 species of *Nectandra* plus 42 presumably related species using two molecular markers, one nuclear and one chloroplast marker.

## ■ MATERIALS AND METHODS

**Taxon sampling.** — In this study, 45 species of *Nectandra* were examined. Among these, there were 7 of the 21 species attributed to the *N. coriacea* group by Rohwer (1993). The remaining 38 *Nectandra* samples include one to six samples from each of the 12 additional morphological groups recognized by Rohwer (1993), plus two species perceived as linking three groups. To explore the intergeneric relationship of the genus within the core Lauraceae, 42 species of the genera *Actinodaphne* Nees, *Aiouea* Aubl., *Aniba* Aubl., *Cinnamomum* Schaeff., *Dicypellium* Nees, *Endlicheria* Nees, *Kubitzkia* van der Werff, *Laurus* L., *Licaria* Aubl., *Lindera* Thunb., *Machilus* Nees, *Neolitsea* (Benth. & Hook.f.) Merr., *Ocotea* Aubl., *Persea* Mill., *Phoebe* Nees, *Pleurothyrium* Nees, *Rhodostemonodaphne* Rohwer & Kubitzki and *Umbellularia* (Nees) Nutt. were also included in the data matrix. Among these, the members of the *Persea* group (*Machilus*, *Persea*, *Phoebe*) were chosen as outgroup taxa. All specimens, their origin and collectors are listed in Appendix 1.

**DNA extraction.** — DNA was isolated from silica-gel dried material or from herbarium specimens with the “innuPREP Plant DNA Kit” (Analytik Jena, Germany) according to the manufacturer’s protocol, with modifications published by Rohwer &

Rudolph (2005). To increase the yield of DNA, the incubation time of the elution step was elongated to 15 min. In addition, a higher temperature of 50°C was applied to improve the solution of the residual DNA from the column.

**PCR amplification and sequencing.** — The whole ITS region (ITS-1–5.8S RNA–ITS-2) and the plastid intergenic region between *psbA* (photosystem II protein D1) and *trnH* (transfer RNA histidine) (*psbA-trnH*) were selected because a particularly high variability was expected in these regions, based on earlier studies (Chanderbali & al., 2001; Kress & al., 2005; Song & al., 2009; Yao & al., 2009; Dong & al., 2012).

The ITS region was amplified according to the general method of White & al. (1990), modified as described in detail by Rohwer & al. (2009). If possible, the entire ITS region was amplified using the primers ITS-18-F (Käss & Wink, 1997, modified by Beyra Matos & Lavin, 1999) and ITS-H (Rohwer & al., 2014). If the PCR failed, smaller PCR products were amplified with primer combinations listed in Table 1.

The chloroplast *psbA-trnH* spacer was amplified using the same conditions, except that dimethyl sulfoxide (DMSO) was not required, because of a much lower GC content. The following primers were used: *psbA* (Sang & al., 1997), *psbA-r1r*, *psbA-r2r* (Heinze, 2007), *trnH* (Tate, 2002) and *trnH-A-8.1* (Klak & al., 2013).

The PCR products were purified with FastAP (Thermo Sensitive Alkaline Phosphatase) and exonuclease I (both enzymes from Thermo Fisher Scientific, Waltham, Massachusetts, U.S.A.) according to the manufacturer’s description. The sequencing reaction and precipitation of the sequencing products were adjusted to the 3500 Genetic Analyzer (Thermo

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

Primer	Direction	Sequence	Author
ITS			
ITS-1	F	5'-TCCGTAGGTGAACCTGCGG-3'	White & al., 1990
ITS-18	F	5'-GTCCACTGAACCTTATCATTTAGAGG-3'	Käss & Wink, 1997; Beyra-Matos & Lavin, 1999
ITS-3	F	5'-GCATCGATGAAGAACGCAGC-3'	White & al., 1990
ITS-D	F	5'-CTCTCGGCAACGGATATCTCG-3'	Käss & Wink, 1997
ITS-L-400	F	5'-CGACTCTCGGCAACGGATATCTC-3'	Rohwer & Rudolph, unpub.
ITS-L-424	F	5'-TAGCGAGATGCGATACGTGG-3'	Rohwer & Rudolph, unpub.
ITS-L-442	F	5'-GGTGTGAATTGCAGAATCCC-3'	Rohwer & Rudolph, unpub.
ITS-4	R	5'-TCCTCGCTTATTGATATGC-3'	White & al., 1990
ITS-CL	R	5'-GCAATTCACACCAMGTATCGC-3'	Rohwer & Rudolph, unpub.
ITS-H	R	5'-CGGTTTCGCTCGCCGTTACTA-3'	Rohwer & al., 2014
ITS-L-459	R	5'-AAGACTCGATGGTTCACGGG-3'	Rohwer & Rudolph, unpub.
<i>psbA-trnH</i> region			
<i>psbA</i>	F	5'-GTTATGCATGAACGTAATGCTC-3'	Sang & al., 1997
<i>psbA-r1r</i>	F	5'-GTAGTAGGTATCTGGTTTACCGCT-3'	Heinze, 2007
<i>psbA-r2r</i>	F	5'-CTTCTTCCTAGCTGCTTGGCCTGT-3'	Heinze, 2007
<i>trnH</i>	R	5'-CGCGCATGGTGGATTACAAAATC-3'	Tate, 2002
<i>trnH-A-8.1</i>	R	5'-TGGATTCACAAATCCACTGC-3'	Klak & al., 2013

Fisher Scientific) as described in Rohwer & al. (2014). The sequences were detected with the automated 3500 Genetic Analyzer as described in the manufacturer's instructions. All samples were sequenced forward and reverse.

**Sequence analysis.** — The quality of the sequences was checked using the program Sequencher v.4.8 (Gene Codes Corporation, 1991–2007). The sequences were edited manually, and a consensus sequence was created by comparison of the forward and reverse sequence chromatogram files of each individual. The consensus sequences and published sequence data retrieved from GenBank (see Appendix 1) were aligned by using the MUSCLE algorithm implemented in MEGA v.6.06 (Tamura & al., 2013), with manual adjustments according to the principles outlined in Rohwer & al. (2014). Potentially informative insertions or deletions (indels) were coded in an indel matrix appended to the DNA sequence matrix, following the rules of simple indel coding (Simmons & Ochoterena, 2000). However, if there were different bases within the same indel position(s), indicating possibly different evolutionary events, we coded a multistate character (0/1/2/3) to account for these differences. Indels that were only ambiguously alignable as well as most of the uninformative indels in the ITS region were excluded from the analysis. Two micro-inversions recognized in the *psbA-trnH* spacer, of 5 and 10 bp, respectively, were reverted, complemented, and initially coded in the 0/1 matrix as well. These characters, however, were later excluded from the analysis, as we had recognized in other Lauraceae (unpub. data) that both orientations were found within at least some species.

**Phylogenetic analysis.** — The nuclear and chloroplast data matrices were analyzed both separately and in combination by maximum parsimony as well as Bayesian inference.

Maximum parsimony analysis was performed in PAUP v.4.0b10 (Swofford, 2001). For heuristic search, 100 random addition sequence replicates, tree bisection-reconnection (TBR), retaining of all minimum length trees (MULTREES=YES) and collapse of zero-length branches were chosen. Gaps were treated as missing data. As the analyses rapidly accumulated more than 200,000 equally parsimonious trees, 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). A full bootstrap, however, with unlimited TBR branch swapping and an unlimited number of trees saved, was not possible with our data, as it quickly ran into overflow. We therefore limited the number of branch exchanges to one million per bootstrap replicate (rearrlimit=1000000).

Bayesian inference was performed using MrBayes v.3.2.2 (Ronquist & al., 2011). The data were separated into a total of five unlinked partitions. Three partitions were applied for the ITS data, (1) for the positions coding for ribosomal RNA (the 5.8S, 18S and 26S regions), (2) for the non-coding ITS-1 and ITS-2 regions, and (3) for ITS-indels. Two additional partitions were used for the *psbA-trnH* data, (4) for the non-coding *psbA-trnH* intergenic region and (5) for the *psbA-trnH*-indels. 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 Jukes-Cantor model was suggested for the ribosomal DNA, possibly due to scarcity of substitutions. The Tamura 3-parameter model was suggested for both spacer regions. Two simultaneous runs of four Metropolis-coupled Monte Carlo Markov chains (MCMCMC) were run for one million generations, saving the current tree every 100 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.

## ■ 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 five rows of Table 2. The aligned genome regions of the combined analysis have a total length of 1240 base pairs (bp). A total of 140 alignment positions were excluded from the analysis. Of the remaining 1100 alignment positions 776 (70.5%) were constant, 164 (14.9%) were variable but parsimony-uninformative and 160 positions (14.5%) were parsimony-informative. The alignment showed 32 parsimony-informative indels having a length of 1–196 bases. Therefore, the final data matrix consisted of 1132 characters, 1100 DNA characters plus 32 indels, encoded using the numbers 0 to 3.

As expected, the results based on each single marker provided (much) less resolution and lower support values than those based on the combined dataset, but they showed only a few cases of significantly supported conflict, mainly due to poor resolution in the results based on the *psbA-trnH* dataset. In the maximum parsimony analyses, we considered 90% bootstrap support (BS) as significant, but the strongest observed conflict was a sister-group relationship of *Cinnamomum japonicum* Siebold with *C. camphora* (L.) J.Presl (90% BS) in the *psbA-trnH* data vs. *C. japonicum* with *C. verum* J.Presl (74% BS) in the ITS data. In each case the respective other species was either the immediate sister taxon (*C. verum* in the *psbA-trnH* data) or placed in a polytomy with the supported species pair. In the Bayesian analyses, where the support values are generally higher, we considered a posterior probability (PP) of

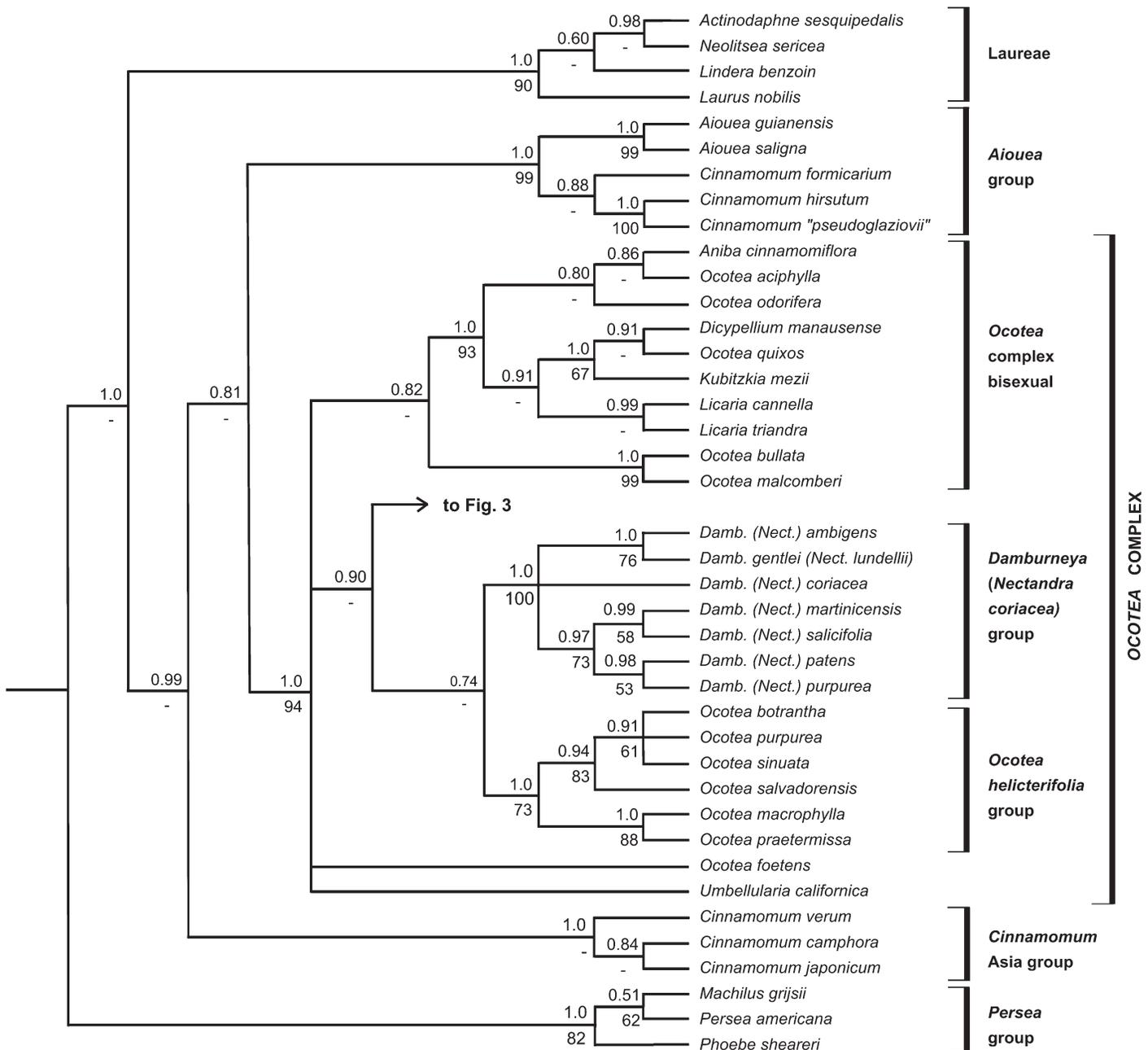
**Table 2.** Statistics of the data matrices and maximum parsimony analyses.

	ITS	<i>psbA-trnH</i>	combined
Total characters (incl. indels)	748	526	1,274
Excluded characters	93	49	142
Constant characters	377	399	776
Uninformative characters	117	47	164
Informative characters	161	31	192
No. of trees	70,000	100,000	39,000
Tree length	675	119	815
Consistency index	0.545	0.714	0.556
Retention index	0.740	0.872	0.749

0.95 as significant. Here we found three cases of conflict, one of them involving the same species as in the MP analyses, but now strongly supported (both PP 1.0). A second conflict was found in the *Nectandra coriacea* group, in the placement of *N. lundellii* C.K.Allen in a polytomy with *N. martinicensis* Mez and *N. salicifolia* (Kunth) Nees in the *psbA-trnH* data (PP 0.96) vs. as sister to *N. ambigens* (S.F.Blake) C.K.Allen in the ITS data (PP 1.0). *Nectandra martinicensis* and *N. salicifolia* were placed in a clade with *N. patens* (Sw.) Griseb. and *N. purpurea* (Ruiz & Pav.) Mez in the ITS data (PP 0.98). A third conflict,

in the placement of *Aniba cinnamomiflora* C.K.Allen, with *Ocotea aciphylla* (Nees) Mez in the ITS data (PP 1.0) vs. with *Kubitzkia mezii* (Kosterm.) van der Werff and the two *Licaria* species in the *psbA-trnH* data (PP 0.94) stayed just below the level of significance in the latter. As these were the only well-supported conflicts, we show only the results based on the combined data (Figs. 2, 3) in this paper. The trees based on the single markers are available in the Electronic Supplement.

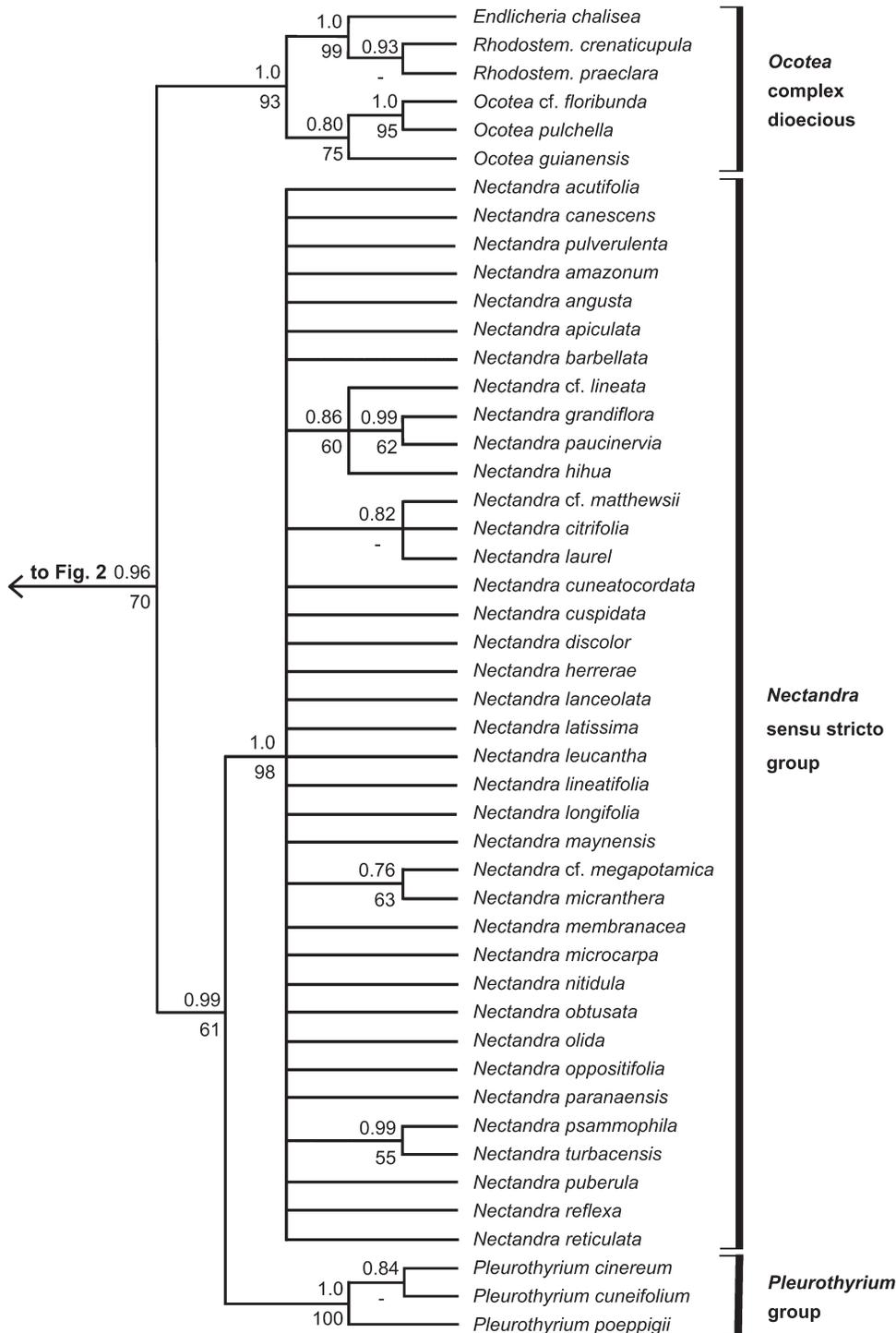
**Maximum parsimony analysis.** — The statistics of the single markers and combined parsimony analyses are shown in



**Fig. 2.** Results of the Bayesian inference using the combined ITS and *psbA-trnH* sequence data matrix. Species of the *Nectandra coriacea* group transferred to *Damburneya*. Posterior probabilities shown above the branches, bootstrap support below. *Damb.* = *Damburneya*, *Nect.* = *Nectandra*. The dioecious species of the *Ocotea* complex, *Nectandra* s.str. and *Pleurothyrium* groups are shown in detail in Fig. 3.

Table 2. The parsimony analysis of the combined data provided 39,000 trees with a length of 815 steps, with a consistency index (CI) of 0.556 and a retention index (RI) of 0.749. Because the bootstrap trees of the maximum parsimony analyses were much less resolved and supported than the trees of the Bayesian inference, only the results of the Bayesian inference of the combined dataset are described in detail in this study. However, two monophyletic groups among the *Nectandra* species

were recognized also by the maximum parsimony analysis with combined markers. The *N. coriacea* group (including *N. ambigens*, *N. coriacea* (Sw.) Griseb., *N. lundellii*, *N. martinicensis*, *N. patens*, *N. purpurea* and *N. salicifolia*; reinstated as *Damburneya* later in this paper) showed a high bootstrap support (BS) of 100%. The *Nectandra* s.str. group, including the remaining 38 species, was less but still significantly supported (98% BS).



**Fig. 3.** Results of the Bayesian inference using the combined markers ITS and *psbA-trnH*, continued from Fig. 2. Posterior probabilities shown above the branches, bootstrap support below. *Rhodostem.* = *Rhodostemonodaphne*.

**Bayesian inference.** — The Bayesian inference of the combined dataset reached convergence at less than 20,000 of one million generations, so that 200 of the 10,001 saved trees (2%) had to be discarded as burn-in. The resulting cladogram is shown in Figs. 2 and 3.

The branch separating the outgroup, viz., the *Persea* group (*Machilus grijsii* Hance, *Persea americana* Mill., *Phoebe shearerii* (Hemsl.) Gamble), from the ingroup is supported with a posterior probability of 1.0. Within the ingroup, the Laureae (*Actinodaphne sesquipedalis* Meisn., *Neolitsea sericea* (Blume) Koidz., *Lindera benzoin* (L.) Blume, *Laurus nobilis* L.; PP 1.0) form the sister group to all remaining taxa (PP 0.99). Among these, the cladogram shows a well-supported Asian *Cinnamomum* group (PP 1.0), whereas its sister group including the remaining taxa is scarcely supported (PP 0.81). Among the latter, a well-supported (PP 1.0) *Aiouea* group, consisting of *Aiouea* and the Neotropical *Cinnamomum* species, is shown as sister to an equally well-supported clade including all other genera, among them *Nectandra* and *Ocotea*.

In the following, this group is called the *Ocotea* complex, as in Chanderbali & al. (2001). Because the aim of this study is to investigate the phylogeny of the genus *Nectandra*, the topology among the other Lauraceae will be not described in detail.

Within the *Ocotea* complex, there is a polytomy, consisting of *Ocotea foetens* (Aiton) Baill., *Umbellularia californica* (Hook. & Arn.) Nutt., a poorly supported clade (PP 0.82) including several species of the *Ocotea* complex, all of them with bisexual flowers, and another weakly supported clade (PP 0.90) including the remaining species. The former clade includes not only species currently placed in *Ocotea*, but also the species of *Aniba*, *Dicypellium*, *Kubitzkia* and *Licaria*. The latter clade then splits into two groups, both of them including species currently placed in *Nectandra*. The smaller of these clades is weakly supported (PP 0.74) and includes several bisexual *Ocotea* species usually attributed to the *Ocotea helicterifolia* group (e.g., in Rohwer, 1991; Van der Werff, 1999: *Ocotea botrantha* Rohwer, *O. purpurea* (Mez) van der Werff, *O. sinuata* (Mez) Rohwer, *O. salvadorensis* (Lundell) van der Werff, *O. macrophylla* Kunth and *O. praetermissa* van der Werff), which form a well-supported monophyletic group (PP 1.00), as sister to the species of the *Nectandra coriacea* group (= *Damburneya*), which form an equally well-supported group. Within the *N. coriacea* group, there is a trichotomy consisting of *N. coriacea* and two well-supported clades, one of them including *N. ambigens* and *N. lundellii* (PP 1.00), the other *N. martinicensis*, *N. salicifolia*, *N. patens* and *N. purpurea* (PP 0.97). *Nectandra martinicensis* and *N. salicifolia* (PP 0.99) form the sister group to *N. patens* and *N. purpurea* (PP 0.98).

The clade including all remaining species is significantly supported (PP 0.96) and splits into a well-supported clade (PP 1.00) consisting of dioecious species only, irrespective of their current generic affiliation (*Endlicheria chalisea* Chanderb., *Rhodostemonodaphne crenaticupula* Madriñán, *Rh. praeclara* (Sandwith) Madriñán, *Ocotea* cf. *floribunda* (Sw.) Mez, *O. pulchella* (Nees) Mez, *O. guianensis* Aubl.) and another well-supported clade (PP 0.99) comprising *Pleurothyrium* and the remaining species of *Nectandra* (i.e., *Nectandra* s.str.). The

genus *Pleurothyrium*, here represented by *P. cinereum* van der Werff, *P. cuneifolium* Nees and *P. poeppigii* Nees, is strongly supported (PP 1.0) as monophyletic.

*Nectandra* s.str. is represented by 38 South American species in our analysis: *N. acutifolia* (Ruiz & Pav.) Mez, *N. amazonum* Nees, *N. angusta* Rohwer, *N. apiculata* Rohwer, *N. barbata* Coe-Teix., *N. canescens* Nees & Mart., *N. citrifolia* Mez & Rusby, *N. cuneatocordata* Mez, *N. cuspidata* Nees & Mart., *N. grandiflora* Nees, *N. discolor* (Kunth) Nees, *N. herrerae* O.C.Schmidt, *N. hihua* (Ruiz & Pav.) Rohwer, *N. lanceolata* Nees & Mart., *N. latissima* Rohwer, *N. laurel* Klotzsch ex Nees, *N. cf. lineata* (Kunth) Rohwer, *N. lineatifolia* (Ruiz & Pav.) Nees, *N. longifolia* (Ruiz & Pav.) Nees, *N. leucantha* Nees & Mart., *N. cf. matthewsii* Meisn., *N. maynensis* Mez, *N. cf. megapotamica* (Spreng.) Mez, *N. membranacea* (Sw.) Griseb., *N. micranthera* Rohwer, *N. microcarpa* Meisn., *N. nitidula* Nees & Mart., *N. obtusata* Rohwer, *N. olida* Rohwer, *N. oppositifolia* Nees & Mart., *N. paranaensis* Coe-Teix., *N. paucinervia* Coe-Teix., *N. psammophila* Nees & Mart., *N. puberula* (Schott) Nees, *N. pulverulenta* Nees, *N. reflexa* Rohwer, *N. reticulata* (Ruiz & Pav.) Mez and *N. turbacensis* (Kunth) Nees. Among these, there is almost no resolution: 27 species and four small clades, with two to four species each, form an extensive polytomy. However, only two species pairs have significant support values (*N. psammophila* and *N. turbacensis*, PP 0.99; *N. grandiflora* and *N. paucinervia*, PP 0.99).

## ■ DISCUSSION

Our results (Figs. 2, 3) show many similarities to those of Chanderbali & al. (2001: fig. 3), but also some differences. As in their study, the *Persea* group, the Laureae, the Cinnamomeae, the Neotropical *Cinnamomum* plus *Aiouea* group, and the *Ocotea* complex are shown as monophyletic groups. The higher support values in our results are due to different methods: Bayesian inference generally leads to higher values than maximum parsimony bootstrap. Within the *Ocotea* complex, further similarities include the presence of (1) a clade consisting of *Aniba*, *Dicypellium*, *Kubitzkia*, *Licaria*, and several bisexual *Ocotea* species, called “*Licaria* group and allies” by Chanderbali & al. (2001), (2) a clade including all dioecious species of the *Ocotea* complex, regardless of their current generic affiliation (*Endlicheria*, *Ocotea*, or *Rhodostemonodaphne*), (3) a clade consisting of *Nectandra* s.str. as sister to *Pleurothyrium*, and (4) a node uniting the two latter clades. The differences between the two studies, e.g., the placement of the *Nectandra coriacea* group relative to the *Ocotea helicterifolia* group and *Umbellularia*, or the position of the Old World species of *Ocotea*, involve only weakly supported nodes.

With an increased taxon sample, we can thus confirm that *Nectandra* in its traditional circumscription is at least paraphyletic with regard to *Pleurothyrium*. The taxonomic consequence of this result, i.e., the formal transfer of the *Nectandra coriacea* group to *Damburneya*, will be drawn below. In addition, *Nectandra* s.str. appears to be closer to the dioecious taxa of

the *Ocotea* complex, whereas the *N. coriacea* group appears to be closer to other, bisexual taxa currently placed in *Ocotea*.

In the past, morphological similarities between *Nectandra* (s.l.), *Ocotea* and *Pleurothyrium* repeatedly led to different opinions regarding the delimitation of the three genera. Schreber (1791) united *Nectandra* and *Ocotea* under the illegitimate name *Porostema*. *Pleurothyrium* was not yet known at that time. It was first described in 1836 by Nees in Lindley (1836). Later in the same year, Nees (1836) published the first monograph of the Lauraceae, in which he repeated the same description on p. 349. He kept not only *Nectandra* and *Pleurothyrium* as separate genera, but also treated species currently placed in *Ocotea* under a variety of different generic names (*Camphoromoea* Nees, *Evonymodaphne* Nees, *Gymnobalanus* Nees & Mart., *Leptodaphne* Nees & Mart., *Mespilodaphne* Nees & Mart., *Ocotea*, *Oreodaphne* Nees & Mart., *Petalanthera* Nees & Mart., *Teleiandra* Nees & Mart.). Some of these will certainly become accepted again once the phylogenetic lineages within the *Ocotea* complex are fully resolved. Meissner (1864) reduced the number of genera by placing *Evonymodaphne*, *Leptodaphne*, *Ocotea*, *Petalanthera*, and *Teleiandra* in the synonymy of *Oreodaphne*, whereas *Camphoromoea*, *Gymnobalanus*, and *Mespilodaphne* were still kept separate. Bentham (1880) placed all of them in *Ocotea*, which has priority over *Oreodaphne* (Aublet, 1775 vs. Nees, 1833). This concept was accepted by Mez (1889), and still remains the most widely used genus concept up to the present. Britton and Millspaugh in their *Bahama Flora* (1920) placed *Nectandra* in the synonymy of *Ocotea*, without any further comment. However, the only species of the *Ocotea* complex occurring in the Bahamas is *Nectandra coriacea*, which is morphologically closer to *Ocotea* than typical *Nectandra* species. In 1952, Kostermans treated *Pleurothyrium* as a section of *Ocotea*, and suggested that also *Nectandra* should be included there. He formally implemented this step in Kostermans (1957). Bernardi (1962) argued that *Nectandra* should be kept separate for pragmatic reasons, because it could easily be identified in the field by looking at the stamens with a hand lens. Also Allen (1966) pleaded in favor of maintaining both *Nectandra* and *Pleurothyrium* as separate genera. Howard (1981) and Liogier (1982), on the other hand, followed Kostermans in treating *Nectandra* as a synonym of *Ocotea*. Both authors, however, were working on the flora of the Antilles, where the more *Ocotea*-like *Nectandra coriacea* group is far more frequent than *Nectandra* s.str. Rohwer & Kubitzki (1985) not only argued in favor of keeping *Nectandra* and *Pleurothyrium* separate from *Ocotea*, but also separated the dioecious species treated as *Nectandra* subg. *Synandrodaphne* by Mez (1889) as the new genus *Rhodostemonodaphne*. The separation of *Rhodostemonodaphne* has been confirmed by subsequent studies (Chanderbali & al., 2001; Madriñán, 2004).

***Nectandra coriacea* group (= *Damburneya*).** — The species of the *N. coriacea* group differ from the remaining *Nectandra* species not only in their DNA sequences, but also morphologically, as pointed out by Rohwer (1993). In his schematic illustration of the perceived morphological similarities, there is only a single dotted line (meant to indicate an uncertain relationship) connecting the *N. coriacea* group to the *N. membranacea* group,

whereas the other major species groups are reticulately connected. However, the apparently best diagnostic characters to separate the *N. coriacea* group from the remaining species are rather inconspicuous and may seem trivial. In the *N. coriacea* group, the adaxial side of the tepals bears at least some more or less straight hairs at the base, often intergrading with crinkled, papillae-like hairs on the distal part. In *Nectandra* s.str., on the other hand, the adaxial side of the tepals is usually papillose throughout, or glabrous at the base and only distally papillose. Likewise, the filaments of stamens and staminodes are almost always pubescent in the *N. coriacea* group, whereas they are glabrous in *Nectandra* s.str. (Fig. 1A, B). Other characters are less diagnostic, but nevertheless helpful to separate the two. The species of the *N. coriacea* group show a mixed to evenly reticulate tertiary leaf venation, like in *Ocotea* (Klucking, 1987), whereas most other *Nectandra* species show distinctly scalariform tertiary venation (Fig. 1C, D). However, there are also a few species of *Nectandra* s.str. showing evenly reticulate venation, e.g., *N. megapotamica*. The filaments are always much narrower than the anthers in the *N. coriacea* group, whereas several species of *Nectandra* s.str. have rather broad filaments, almost as broad as the anthers. Most species of *Nectandra* s.str. have anthers with a prolonged triangular apex or at least an apiculate tip, whereas this is never found in the *N. coriacea* group. Here the anthers are apically broadly rounded, truncate, or even slightly emarginate. In addition, they are mostly smooth or only slightly papillose, whereas they are strongly papillose in most species of *Nectandra* s.str. (Fig. 1E–J).

***Nectandra* s.str.** — *Nectandra* s.str. is not only confirmed as a well-supported monophyletic entity in our phylogenetic analysis, it is also easily characterized by a large deletion in the *psbA-trnH* spacer, of ca. 160 bp compared to its sister group *Pleurothyrium*, and of a similar magnitude compared to all other genera of Lauraceae investigated so far. This deletion might even be used as an identification tool for sterile collections: if the amplification product between *psbA* and *trnH* is about 340 bp long, then it is *Nectandra* s.str., if it is about 500 bp long, it belongs to other Lauraceae.

In morphological terms, *Nectandra* becomes more clearly definable by exclusion of the *N. coriacea* group. It comprises species with (sub)equal tepals that are papillose but not pubescent on their adaxial side, with nine fertile stamens with glabrous filaments and papillose, often apically prolonged anthers, in which the four pollen sacs are arranged collaterally or in a shallow arc. In addition, the leaves of most species show a scalariform tertiary venation.

The internal topology of *Nectandra* s.str. is largely unresolved in our analyses, apart from a few scarcely supported clades and three well-supported species pairs. Some of them seem to correspond to the morphological groups of Rohwer (1993) while others do not. At this point, however, it makes little sense to discuss even the better supported groups, because of the generally poor resolution and occasional uncertainties in the determination of sterile or fruiting collections.

**Biogeography of *Nectandra* s.l.** — The results of the present phylogenetic study showed that it was not possible to resolve the phylogenetic lineages within *Nectandra* s.str. However, with the

same marker set a more distinct resolution in the *N. coriacea* group could be achieved. While this result may be influenced by the unequal number of species in the two groups, it may also be interpreted in terms of the biogeography of this genus.

On the basis of fossil records from North, Central and South America it is conceivable to sketch a hypothetical scenario of migration from North to South America, similar to the one suggested for the *Cinnamomum*-like Lauraceae by Huang & al. (2016). It should be kept in mind, however, that the assignment of fossils to *Nectandra* should be assessed with caution. In the first half of the 20th century it was common practice to assign fossil plants to recent groups due to superficial similarities (Kvaček, 1971). As pointed out by Christophel & al. (1996), the overall leaf morphology and the venation patterns may be quite similar in species of different genera.

The first fossils attributed to *Nectandra*, *N. antillanifolia* E.W.Berry, *N. arkansana* E.W.Berry and *N. pseudocoriacea* E.W.Berry, date from the Eocene and were found in North America (Berry, 1924, 1931). According to marine and terrestrial records, the Early Eocene Climatic Optimum (EECO, 52.0 to 50.0 Ma) was the warmest period of the Tertiary, with temperatures permanently above freezing even in British Columbia (Greenwood & Wing, 1995; Zachos & al., 2001; Hamann & Wang, 2005, 2006; Huber & Caballero, 2011; Hyland & Sheldon, 2013). After the EECO there was a global cooling tendency, with two cooling intervals in the Early to Middle (50 to 48 Ma) and Late Eocene (40 to 36 Ma), interrupted by an episodic warming (Middle Eocene Climatic Optimum, MECO, ca. 41.5 Ma) (Zachos & al., 2001; Bohati & Zachos, 2003; Bijl & al., 2010).

A working hypothesis for future studies may be that the progenitors of the *N. coriacea* group were displaced to Central America during one of the Eocene cooling periods. There they were able to re-establish and diversify. A *Nectandra*-like fossil from the Culebra Cut in Panama, estimated to be of Eocene to Oligocene age (Berry, 1914), may be considered as evidence of this migration pathway. The diversification of the mainly South American *Nectandra* s.str. occurred much later, presumably in the Miocene (18±5 Ma) according to the molecular clock analysis of Chanderbali & al. (2001). However, the estimate of Chanderbali & al. is based on just one molecular marker (ITS), and only a single species of *Nectandra*, *N. amazonum*, so that the results have to be regarded as rather preliminary. On the other hand, it is consistent with the fact that first fossils from South America ascribed to *Nectandra*, *N. areolata* Engelh., *N. chiliana* E.W.Berry, *N. patagonica* E.W.Berry and *N. saltensis* Anzótégui, date from the Miocene (23.0 to 5.3 Ma) (Berry, 1922, 1925, 1936; Anzótégui & Aceñolaza, 2008).

Assuming a nearly identical DNA mutation rate in the non-coding genomic regions, such an age difference between the two *Nectandra* clades (Figs. 2, 3) could explain the different degree of resolution within the two groups with the same molecular marker.

**Biogeographic diversification in South America.** — An exchange of species between the two subcontinents appears to have been possible repeatedly, e.g., via the “proto-Greater Antilles”, which may have provided an island corridor in the Middle to Late Eocene for diverse plant species as already

discussed by Gentry (1982), Savage (1982), Iturralde-Vinent & MacPhee (1999) and Pennington & Dick (2004).

The emergence of the Panamanian Isthmus in the Miocene (11.62 to 15.97 Ma) (Montes & al., 2015) facilitated the exchange of species considerably. Also the hypothetic ancestor of *Nectandra* s.str., *Pleurothyrium* and a part of the *Ocotea* complex may have colonized the South American continent after the opening of the direct land route. In South America, *Nectandra* s.str. appears to have undergone an extensive and rapid radiation. The drivers of this radiation are still unclear, but they may have been related to the opening of new habitats by geological events.

New habitats certainly have been created by the formation of the Andes from late Oligocene to early Miocene (Hoorn & al., 2010; Folguera & al., 2011). Thereby the diversity of habitats in South America increased, forcing the diversification of many taxa, including *Nectandra*. After all, *Nectandra* is found in most wet to seasonally dry forests in tropical America, from sea level to about 3000 m elevation, and from the flooded forests of the Amazon to the relatively dry Cerrado savanna forests of Brazil.

## ■ TAXONOMIC CONSEQUENCES

As described above, *Nectandra* in its current circumscription has turned out to be diphyletic, so that it cannot be treated as a single genus any more. The type, *N. sanguinea* Rol., is morphologically clearly a member of the group called *Nectandra* s.str. above. Therefore, the species of the *N. coriacea* group need to be transferred to a different genus. The oldest genus name validly published for a species of the *N. coriacea* group is *Damburneya* Raf. (Rafinesque, 1838), which therefore has to be adopted as the accepted name of this group.

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

Trees or shrubs. Leaves evergreen, alternate, penninerved, with ± evenly reticulate to mixed (not scalariform) tertiary venation. Flowers trimerous, bisexual. Tepals six, (almost) equal, abaxially glabrous or pubescent, adaxially pubescent at the base and (usually strongly) papillose towards the tip, dropping off as a ring after anthesis. Fertile stamens 9, with distinct, pubescent filaments. Anthers transverse-elliptic to almost rectangular, apically rounded to truncate, never apiculate or triangular, with 4 pollen sacs, mostly arranged in a shallow arc but sometimes in two pairs, one above the other. Staminodes 3, with pubescent filament and a distinct glandular head, the latter usually ± rhomboidal, rarely sagittate. Ovary inserted in a shallowly bowl-shaped to cup-shaped receptacle. Fruit almost completely exerted, on a shallowly bowl-shaped to turbinate cupule.

Distribution: Mainly Central America, with a few species reaching North America (Mexico: Sinaloa and Tamaulipas; U.S.A.: Florida), the Antilles and Bahamas, as well as northern and northwestern South America, and one species (*D. purpurea*) reaching Bolivia and Espirito Santo in Brazil.

In the description of *Damburneya* Rafinesque (1838) cited “Type *D. maritima* Raf. *Laurus catesbei* Mx. auct.” This could

be interpreted either as *Laurus catesbyana* Michx., although other authors wrote “*catesbei*”, or as “what other authors interpreted as *Laurus catesbyana* Michx., but this is a different species.” We do not know if the spelling “*catesbei*” has been used at all. The spelling that comes closest to it is “*catesbaei*”, used by Persoon (1805) and by Nuttall (1818). This, however, refers to the same species, as Persoon cited “Michaux. p. 244. Catesb. II. t. 28.” (see below).

Michaux (1803) had described *Laurus catesbyana*, citing “Catesb. II. t. 28.” and giving the information “Hab. in Florida calidiore et Bahama.” The literature citation refers to Catesby (1754), *The natural history of Carolina, Florida, and the Bahama Islands*, vol. 2. Plate 28 of this work shows a plant with apparently racemose inflorescences bearing white, rotate, mostly hexamerous flowers, ovate-lanceolate leaves, and fruits with a turbinate red cupule that resemble those of the species currently known as *Nectandra coriacea* (Sw.) Griseb. On the preceding page, the species is described as “*Cornus, foliis Salicis Laureae acuminatis; floribus albis; fructu Sassafras.*” Catesby gives no information about the origin of the plant, but there is no other species with similar morphology in the general area treated in his book. Moreover, a specimen in P (barcode P00128647), bearing a label “Herbarium Richard. *Laurus catesbyana*. Michaux—Florida calidior”, has been annotated as *Nectandra coriacea* (Sw.) Griseb. by Rohwer in 1984. Rohwer (1993) accepted this specimen as the holotype of *Laurus catesbyana*. However, Howard & Staples (1983) had already lectotypified the species by stating “Catesby’s plate is the type of *Laurus catesbyana* Michx.”

*Damburneya* includes the following species:

1. ***Damburneya ambigens*** (S.F.Blake) Trofimov, **comb. nov.** ≡ *Phoebe ambigens* S.F.Blake in Contr. U.S. Natl. Herb. 24 (1): 3–4. 1922 ≡ *Nectandra ambigens* (S.F.Blake) C.K. Allen in J. Arnold Arbor. 26: 371–372. 1945 – Holotype: Honduras. Copán: Rodezno, 120 m, 3 May 1919, *Whitford & Stadtmiller 7* (US [#989623 according to Blake, n.v.]; isotypes: US barcode 00028324! [stamped 989622, and with note “see other sheet”], WIS barcode 00000343MAD [photo!]).  
= *Nectandra venosissima* Lundell in Wrightia 4(3): 106–107. 1969 ≡ *Ocotea venosissima* (Lundell) Lundell in Wrightia 5(9): 341. 1977 – Holotype: Guatemala. Petén, La Cumbre, west of km. 145 of Cadenas Road, 15 May 1967, *Contreras 6915* (LL barcode 00370901 [photo!]; isotypes: K barcode K000576145!, LL barcode 00370902!, MO barcode MO-287545!, MSC barcode MSC0092454 [photo!], NY barcode 00355398 [photo!], S No. S-R-7243 [photo!]).
2. ***Damburneya bicolor*** (Rohwer) Trofimov & Rohwer, **comb. nov.** ≡ *Nectandra bicolor* Rohwer in Fl. Neotrop. Monogr. 60: 79–81, fig. 20. 1993 – Holotype: Panama. Panama: Vic. Cerro Jefe, 09°15'N, 79°30'W, 850 m, 24 Jul 1986 (fl), *McPherson 9804* (HBG barcode HBG-509899!; isotypes: F barcode v0061453F!, MO barcode MO-215831!, PMA barcode 347 [photo!]).

3. ***Damburneya colorata*** (Lundell) Trofimov, **comb. nov.** ≡ *Nectandra colorata* Lundell in Wrightia 4(1): 33. 1968 – Holotype: Guatemala. Petén: 1 km NW of Cadenas, bordering Río Sarstun, 10 Aug 1967 (fl), *Contreras 6999* (LL barcode 00370880!; isotypes: CAS barcode 00036351!, LL barcode 00370881!, MSC barcode MSC0092443 [photo!], MEXU barcode MEXU 00137658 [photo!], NY barcode 00355382 [photo!], S No. S-R-7209 [photo!]).
4. ***Damburneya coriacea*** (Sw.) Trofimov & Rohwer, **comb. nov.** ≡ *Laurus coriacea* Sw., Prodr.: 65. 1788 ≡ *Oreodaphne coriacea* (Sw.) Nees, Syst. Laur.: 454. 1836 ≡ *Nectandra coriacea* (Sw.) Griseb., Fl. Brit. W. I.: 281. 1860 ≡ *Ocotea coriacea* (Sw.) Britton in Britton & Millspaugh, Bahama Fl.: 143. 1920 – Lectotype (first-step designated by Imkhanitskaya in Novosti Sist. Vyssh. Rast. 11: 201. 1974; second-step designated by Rohwer in Greuter & Rankin Rodríguez, Fl. Rep. Cuba, fasc. 19: 50. 2014): Jamaica. Without locality, *Swartz s.n.* (S No. S-R-3160!; isolectotypes: G-DC!, LD barcode 1263945 [photo!], S Nos. S09-16123! & S09-16328 [photo!], SBT barcode SBT11586 [photo!]; possible isolectotype: BM barcode BM000758871!).  
= *Laurus catesbyana* Michx., Fl. Bor.-Amer. 1: 244–245. 1803 (“*Catesbyana*”) ≡ *Gymnobalanus catesbyanus* (Michx.) Nees, Syst. Laur.: 483. 1836 ≡ *Damburneya maritima* Raf., Sylva Tellur.: 136. 1838, nom. illeg. ≡ *Persea catesbyana* (Michx.) Chapm., Fl. South. U.S.: 393–394. 1860 ≡ *Nectandra catesbyana* (Michx.) Sarg. in Gard. & Forest 2: 448. 1889 ≡ *Ocotea catesbyana* (Michx.) Sarg., Silva 7: 11, t. 303. 1895 – Lectotype (designated by Howard & Staples in J. Arnold Arbor. 64: 528. 1983): [illustration in] Catesby, Nat. Hist. Carolina 2: t. 28 1734.  
= *Nectandra willdenoviana* Nees, Syst. Laur.: 321. 1836, non ibid. p. 290 ≡ *Nectandra neesii* D.Dietr., Syn. Pl. 2: 1646. 1840, nom. illeg. superfl. ≡ *Nectandra anonyma* Steud., Nomencl. Bot., ed. 2, 2: 187. 1841, nom. illeg. superfl. – Holotype: “absque nomine et patriae indicatione” (B!, fragments: GZU barcode GZU000254297!).  
= *Nectandra boniato* A.Rich. in Sagra, Hist. Fis. Cuba, Bot. 11: 188. 1850 ≡ *Nectandra earlei* Britton ex Roig & Acuña in Revista Soc. Cub. Bot. 6(2–3): 17. 1949, nom. illeg. superfl. – Lectotype (first-step designated by Rohwer in Fl. Neotrop. Monogr. 60: 50. 1993; second-step designated by Rohwer in Greuter & Rankin Rodríguez, Fl. Rep. Cuba, fasc. 19: 50. 2014): Cuba. Province not indicated: Near Guanamar, *de la Sagra s.n.* in Herb. Richard (P barcode P00128644!; isolectotypes: P barcodes P00128645! & P00128646!).  
= *Nectandra cigua* A.Rich. in Sagra, Hist. Fis. Cuba, Bot. 11: 187. 1850 – Lectotype (designated by Rohwer in Fl. Neotrop. Monogr. 60: 50. 1993): Type: Cuba. “St Yago de Cuba”, 1844, *Linden 1715* (P barcode P00267848!; isolectotypes: BM barcodes BM000758770! & BM000900949!, BR barcode 0000005114146 [photo!], G!, NY!, P!).  
= *Nectandra willdenoviana* var. *latifolia* Meisn. in Candolle, Prodr. 15(1): 165. 1864 – Lectotype (designated by Rohwer

- in Fl. Neotrop. Monogr. 60: 50. 1993): Puerto Rico. Without locality, *Ruiz & Pavón s.n.* (G barcode G00369069!; isolectotype: BM barcode BM000947295!).
- = *Nectandra willdenoviana* var. *obliterata* Meisn. in Candolle, Prodr. 15(1): 165. 1864 – Holotype: Jamaica. Near Spanish Town, *Hartweg 1566* (K barcode K000576162!; isotypes: BM barcode BM000758757!, G barcode G00369072!, K barcode K000576165!, MEL barcode MEL 2390006 [photo!], OXF!).
- = *Ocotea lundellii* Standl. in Publ. Carnegie Inst. Wash. 461(4): 56. 1935 – Holotype: Guatemala. Petén: Ixlu ruins, Lake Petén, 15 Jun 1933 (fl), *Lundell 4359* (F barcode v0075494F!; isotypes: CAS barcode 0003650 [photo!], G barcodes G00369070! & G00369071!, LL barcode 00370916 [photo!], K barcode K000576137 [photo!], MICH barcode 1210258 [photo!]; fragment: A barcode 00042041 [photo!]).
- The two syntypes of *Nectandra willdenoviana* var. *latifolia*, *Ruiz & Pavón s.n.* and *Sieber 312*, are very different from one another. The latter collection is placed in *Damburneya patens* here (cf. Rohwer, 1993: 56). Additional syntypes of *N. cigua*: Cuba. Without locality, *de la Sagra s.n.* (COL barcode COL000001384 [photo!], K barcode K000576167!, P barcodes P00128641, P00128642 & P00128643 [photos!], S No. S-R-7206); Cuba. Alquinar, Apr 1829, *de la Sagra 235* (NY barcodes 00074384 & 00074385).
5. *Damburneya cufodontisii* (O.C.Schmidt) Trofimov & Rohwer, **comb. nov.** ≡ *Ocotea cufodontisii* O.C.Schmidt in Arch. Bot. (Forli) 11(1): 50–51. 1935 ≡ *Nectandra cufodontisii* (O.C.Schmidt) C.K.Allen in J. Arnold Arbor. 26: 393–394. 1945 – Holotype: Costa Rica. San José: Volcan Irazú, SW slope, pass towards San Isidro, 2000 m, 30 May 1930 (fl), *Cufodontis 315* (B barcode B 10 0185085!; isotype: F barcode v0061541F!).
- = *Ocotea seibertii* C.K.Allen in J. Arnold Arbor. 26: 336. 1945 – Holotype: Costa Rica. Alajuela: Above Lecheria on Poás, 2300 m, 30 Jul 1932 (fl), *Stork 3377* (F barcode v0061558F!; isotype: UC barcode UC 1214729!).
6. *Damburneya gentlei* (Lundell) Trofimov, **comb. nov.** ≡ *Persea gentlei* Lundell in Contr. Univ. Michigan Herb. 6: 18. 1941 ≡ *Phoebe gentlei* (Lundell) Standl. & Steyererm. in Publ. Field Mus. Nat. Hist., Bot. Ser. 23(3): 117. 1944 ≡ *Nectandra lundellii* C.K.Allen in J. Arnold Arbor. 26: 381–382. 1945 (“*Lundellii*”) – Holotype: Belize. Stann Creek Dist.: Stann Creek Valley, Mountain Cow Ridge, 30 Mar 1940 (fl), *Gentle 3288* (MICH barcode 1210255 [photo!]; isotypes: CAS barcode 0003917 [photo!], F barcode v0061718F!, LL barcodes 00256894, 00256895 & 00370931 [photos!], NY barcode 00355807!, US barcodes 00099116 [photo!] & 00997561!).
7. *Damburneya leucocome* (Rohwer) Trofimov & Rohwer, **comb. nov.** ≡ *Nectandra leucocome* Rohwer in Fl. Neotrop. Monogr. 60: 90. 1993 – Holotype: Mexico. Chiapas: NW of Santa Margarita (S of La Arena), 80 m, 16 ma [sic!] 1960 (fl), *A. Gomez P. 302* (US barcode 00288878!).
8. *Damburneya longicaudata* (Lundell) Trofimov & Rohwer, **comb. nov.** ≡ *Phoebe longicaudata* Lundell in Bull. Torrey Bot. Club 64: 548–549. 1937 ≡ *Nectandra longicaudata* (Lundell) C.K.Allen in J. Arnold Arbor. 26: 383–384. 1945 – **Lectotype** (first-step designated by Rohwer in Fl. Neotrop. Monogr. 60: 66. 1993; **second-step, designated here**): Belize. El Cayo Dist.: Near San Agustín, Mountain Pine Ridge, Aug 1936 (fl), *Lundell 6833* (MICH barcode 1002614A!; isolectotype: MICH barcode 1002614B!).
- = *Phoebe savannarum* Standl. & Steyererm. in Publ. Field Mus. Nat. Hist., Bot. Ser. 23(3): 118. 1944 ≡ *Nectandra savannarum* (Standl. & Steyererm.) C.K.Allen in J. Arnold Arbor. 26: 382–383. 1945 – Holotype: Guatemala. Alta Verapaz: South of savanna between base of Cerro Chinajá at Sachaj and Sacacao, 150–180 m, 6 Apr 1942 (fl), *Steyermark 45712* (F!; fragments: A barcode 00246780, LL barcode 00370953 [photo!]).
- Additional syntypes of *Phoebe longicaudata*: Belize, El Cayo Dist., Mountain Pine Ridge, San Agustín, Jul–Aug 1936, *Lundell 6757* (MICH barcode 1104613!, NY barcode 00355891 [photo!], US barcode 00028323 [photo!]).
9. *Damburneya longipetiolata* (van der Werff) Trofimov & Rohwer, **comb. nov.** ≡ *Nectandra longipetiolata* van der Werff in Fieldiana Bot., n.s., 23: 60. 1990 – Holotype: Costa Rica. Limón: Hitoy Cerere reserve, SW of Valle La Estrella, along Río Cerere to ca. 1 km upstream from Quebrada Barrera, 09°40.5'N, 83°02'W, 90–200 m, 31 Jul 1985 (fl), *Grayum 5769* (MO barcode MO-287976!; isotypes: F barcode v0077722F [photo!], MEXU barcode MEXU 00678703 [photo!], PMA barcode 778 [photo!]).
10. *Damburneya martinicensis* (Mez) Trofimov, **comb. nov.** ≡ *Nectandra martinicensis* Mez in Mitt. Bot. Vereins Kreis Freiburg 47/48: 421. 1888 – Lectotype (designated by Bernardi in Candollea 22: 72. 1967, see Rohwer, 1993): Trinidad. Without locality, *Sieber Fl. Trinitatis 99* (G barcode G00369042!; isolectotypes: B barcodes B 10 0185042!, B 10 0185043! & B 10 0185044!, BM barcode BM000947298!, E barcode E00259378 [photo!], F barcode v0061472F!, K!, L!, LE barcodes LE 00006788 [photo!], LE 00006789 [photo!] & LE 00006790 [photo!], M barcode M-0147285!, MEL barcode MEL 2390507 [photo!], MO barcode MO-277524!, OXF!, P barcode P01961740!)
- = *Nectandra tabascensis* Lundell in Lloydia 4: 48. 1941 ≡ *Ocotea tabascensis* (Lundell) Howard in J. Arnold Arbor. 62: 58. 1981 – Holotype: Mexico. Tabasco: La Palma, on the San Pedro de Martir River near the Petén border, 1–6 Jun 1939 (fl), *Matuda 3299* (MICH barcode 1104584 [photo!]; isotypes: CAS barcode 0003640 [photo!], F barcode v0061466F!, LL barcode 00370898 [photo!], MEXU barcode MEXU 00132946 [photo!], NY!).
- = *Nectandra glandulifolia* Lasser in Bol. Técn. Minist. Agric. 3: 16. 1942 – Holotype: Venezuela. Miranda: Hacienda El Volcán, near Santa Lucia, 300 m, 10–16 Nov 1918 (fl), *Pittier 8270* (VEN barcode 290505 [photo!]; isotypes:

F barcode v0061500F!, GH barcode 00041941 [photo!],  
US barcode 00048364!).

= *Nectandra woodsoniana* C.K. Allen in J. Arnold Arbor. 26: 380. 1945 – Holotype: Costa Rica. San José: Potrero of Don José Barrantes, near San Isidro del General, 730 m, 30 Jun 1932 (fl), *Stork 3059* (F barcode v0061467F!, fragment: A barcode 00041915 [photo!]).

Additional syntypes of *Nectandra martinicensis*: Panama, Paraiso Sta. P.R.R., Jul 1861, *Hayes 400* (E barcodes E00259379 [photo!], E00259380 [photo!] & E00259381 [photo!], BR barcode 000005115600 [photo!]).

11. *Damburneya matudae* (Lundell) Trofimov & Rohwer, **comb. nov.** ≡ *Nectandra matudae* Lundell in Wrightia 1(2): 149. 1946 – Holotype: Mexico. Chiapas: Malpaso, near Siltepec, 1000 m, 21 Jul 1941 (fl), *Matuda 4522* (LL barcode 00370889 [photo!]; isotypes: F!, MO barcode MO-285176!, NY!, US barcode 00099288!).

= *Nectandra glandulosa* Lundell in Wrightia 1(2): 148. 1946 ≡ *Pleurothyrium glandulosum* (Lundell) Lundell in Wrightia 5(9): 344. 1977 – Holotype: Mexico. Chiapas: Montecristo, 1350 m, 17 Jun 1945 (fl), *Matuda 5934* (LL barcode 00370884!; isotypes: K barcode K000602146!, LL barcode 00370885 [photo!], MEXU barcode MEXU 00081106 [photo!], MO barcode MO-285175!, UC barcode UC 796248 [photo!], US barcode 00099281!).

12. *Damburneya miraflores* (van der Werff) Trofimov & Rohwer, **comb. nov.** ≡ *Nectandra miraflores* van der Werff in Ann. Missouri Bot. Gard. 75: 410. 1988 – Holotype: Nicaragua. Jinotega: 30 km E of Esteli, Laguna de Miraflores, 1200 m, 12 May 1976 (fl), *Neill 329 = 7204* (MO barcode MO-285158!; isotype: MO barcode MO-357846!).

13. *Damburneya nitida* (Mez) Trofimov & Rohwer, **comb. nov.** ≡ *Nectandra nitida* Mez in Jahrb. Königl. Bot. Gart. Berlin 5: 461. 1889 – Lectotype (designated by Rohwer in Fl. Neotrop. Monogr. 60: 63. 1993): Panama. Canal Zone: Barbacoas Station, P.R.R., May 1861 (fl), *Hayes 133* (K barcode K000644167!; isolectotypes: BM barcodes BM000947222! & BM000947223 [photo!]).

= *Nectandra perdubia* Lundell in Lloydia 4(1): 47. 1941 – Holotype: Mexico. Tabasco: Boca Cerro, Tenosique 1–5 Jul 1939 (fl), *Matuda 3576* (MICH barcode 1104577 [photo!]; isotypes: F barcode v0061459F!, MEXU barcode MEXU 00013215 [photo!], NY!).

Additional syntypes of *Nectandra nitida*: Mexico, *Haenke s.n.* (B barcode B 10 0247370!, GOET barcode GOET004518!).

14. *Damburneya patens* (Sw.) Trofimov, **comb. nov.** ≡ *Laurus patens* Sw., Prodr.: 65. 1788 ≡ *Ocotea patens* (Sw.) Nees, Hufeland. Ill.: 10. 1833 ≡ *Phoebe patens* (Sw.) Nees, Syst. Laur.: 117. 1836 ≡ *Nectandra patens* (Sw.) Griseb., Fl. Brit. W. I.: 281. 1860 – Holotype: Jamaica. Without locality, *Swartz s.n.* (S No. S-R-3170!; isotype: G-DC!; possible isotypes: BM barcode BM000758873!, C!).

= *Laurus exaltata* Sw., Prodr.: 65. 1788 ≡ *Oreodaphne exaltata*

(Sw.) Nees, Hufeland. Ill.: 16. 1833 ≡ *Nectandra exaltata* (Sw.) Griseb., Fl. Brit. W. I.: 281. 1860 ≡ *Ocotea exaltata* (Sw.) Proctor in J. Arnold Arbor. 63: 241. 1982 – **Lectotype (designated here)**: Jamaica. Without locality, *Swartz s.n.* (S No. S-R-3161!; isolectotypes: G-DC!, S No. S09-16127!; possible isolectotype: C!).

= *Nectandra coriacea* f. *dubia* Mez in Jahrb. Königl. Bot. Gart. Berlin 5: 461. 1889 – Lectotype (designated by Rohwer in Fl. Neotrop. Monogr. 60: 54. 1993): Windward Islands. Martinique: Fort Desaix, Rivière Madame, *L. Hahn 902* (G!; isolectotypes: BM barcode BM000900930!, BR barcode 00000517610!, E barcode E00259377 [photo!], K barcode K000576166 [photo!], P barcodes P00711147!, P00711148! & P00711149!).

= *Ocotea jamaicensis* Mez in Bull. Herb. Boissier, sér. 2, 5: 241. 1905 – Lectotype (designated by Rohwer in Fl. Neotrop. Monogr. 60: 54. 1993): Jamaica. Portland: Blue Mountains, 25 Jul 1894 (fl juv, fr), *W. Harris 5267* (B barcode B 10 0086156!; isolectotypes: B barcode B 10 0086155!, BM barcode BM000758642!).

= *Tylostemon angustitepalus* K. Krause in Bot. Jahrb. Syst. 53: 450. 1915 ≡ *Ocotea angustitepala* (K. Krause) Robyns & R. Wilczek in Bull. Jard. Bot. État Bruxelles 20: 213. 1950 – Holotype: Cameroon. Near Victoria, probably cultivated, Jun 1912 (fl), *Deistel 559* (B barcode B 10 0277550!; isotype: B barcode B 10 0277549!).

Additional syntypes of *Ocotea jamaicensis*: Jamaica, Blue Mountains, *Harris 5114* (B barcode B 10 0086154!; isosyntypes: BM barcode BM000758640!, NY barcode 00074417!, P barcode P00267888!).

*Tylostemon angustitepalus* K. Krause was described from supposedly primary forest (“Urwald”) near Victoria (now Limbe) in Cameroon. However, there was a botanical garden associated with the agricultural station at Victoria, where species from all over the world have been cultivated. To our knowledge, the species has never again been collected in Africa. Therefore, we are reasonably sure that it was described from a single cultivated tree, and Cameroon is not part of the natural distribution of the genus.

15. *Damburneya purpurea* (Ruiz & Pav.) Trofimov, **comb. nov.** ≡ *Laurus purpurea* Ruiz & Pav., Fl. Peruv. 4: t. 351. [1804–1813?] ≡ *Nectandra purpurea* (Ruiz & Pav.) Mez in Jahrb. Königl. Bot. Gart. Berlin 5: 443. 1889 – Lectotype (designated by Bernardi in Candollea 22: 60. 1967, as “specimine holotypico herbarii berlinensis addicto”): Peru. Huánuco, “in Andium nemoribus ad Cuchero et Chinchao”, 1778, *Ruiz & Pavón s.n.* (B barcode B 10 0185160!; isolectotypes: BM barcode BM000947299!, F barcode v0040316F!, G barcode G00369268!, MA barcode MA 811806!, OXF!).

= *Ocotea latifolia* Kunth in Humboldt & al., Nov. Gen. Sp. 2: 131 [folio ed.] or 165 [quarto ed.]. 1817 ≡ *Persea latifolia* (Kunth) Spreng., Syst. Veg. 2: 270. 1825 ≡ *Nectandra latifolia* (Kunth) Mez in Jahrb. Königl. Bot. Gart. Berlin 5: 454–455. 1889 – Holotype: Colombia. Cundinamarca, “in alta planitie Bogotensi”, *Humboldt & Bonpland s.n.* (P barcode P00128755!).

- = *Nectandra polita* Nees & Mart., Syst. Laur.: 325–326. 1836 – Holotype: Brazil. Bahia, Cachoeira, “in sylvis Capões ad Villa da Caxoeira”, Nov 1818, *Martius s.n.* (M barcode M-0121031!; isotype: GZU barcode GZU000249355!).
- = *Nectandra polita* var. *oerstedii* Meisn. in Candolle, Prodr. 15(1): 164. 1864 – Holotype: Nicaragua. “Ad Granada”, *Oersted 12* (B barcode B 10 0185158!).
- = *Ocotea flexuosa* Rusby, Descr. S. Amer. Pl.: 21. 1920 – Holotype: Colombia. Magdalena, Santa Marta, 14 Jan, *H.H. Smith 1764* (NY barcode NY00355604!; isotypes: BM barcode BM000993966!, CM barcode 0648 [photo!], F barcode v0061597F!, GH barcode 00042096!, K barcode K000602440! [dated July 1903], MICH barcode 1104593 [photo!], MO barcode MO-247435!, P barcodes P00711026! & P00711052!, PH barcode 00019563 [photo!], US barcode 00099214!).

Rohwer (1986) considered *Nectandra latifolia* (Kunth) Mez as the correct name of this species, because the text of the *Laurographia (Flora Peruviana, et Chilensis, vol. 4)*, containing the description of the competing name *Laurus purpurea* Ruiz & Pav. remained unpublished until 1955. However, the plates have been distributed earlier, and the plate of this species shows floral details and a separate fruit. According to Art. 38.8/38.9 of the *Code* (McNeill & al., 2012), this is sufficient for valid publication. According to Alvarez López (1955), the plates have been ready for distribution in late 1803 or early 1804, but it remained unclear when they actually had been distributed. Stafleu & Cowan (1979) suggested “In view of the circumstance that the first references to Ruiz and Pavon’s fourth volume date from 1830, it seems advisable to regard the publication by Kunth as the earlier one.” Now Pedro Moraes (pers. comm.) has drawn our attention to the fact that Pavón sent a copy of the *Laurographia* and the plates to J.E. Smith in July 1813, for presentation to the Linnean Society of London. The accompanying letter is available at <http://linnean-online.org/62228>. This can be regarded as an effective publication in the sense of Art. 30.4./30.5. of the *Code* (McNeill & al., 2012).

16. *Damburneya rudis* (C.K.Allen) Trofimov & Rohwer, **comb. nov.** ≡ *Nectandra rudis* C.K.Allen in J. Arnold Arbor. 26: 401–402. 1945 – Holotype: Mexico. Chiapas: Mt. Ovando, 29 Dec 1936 (fl), *Matuda 470* (A barcode 00041905!; isotypes: LL barcode 00370896 [photo!], MICH barcode 1104580 [photo!], US barcode 00028316!, WIS barcode v0255265WIS [photo!]).
17. *Damburneya salicifolia* (Kunth) Trofimov & Rohwer, **comb. nov.** ≡ *Ocotea salicifolia* Kunth in Humboldt & al., Nov. Gen. Sp. 2: 132 [folio ed.] or 166 [quarto ed.]. 1817 ≡ *Persea salicifolia* (Kunth) Spreng., Syst. Veg. 2: 270. 1825 ≡ *Nectandra salicifolia* (Kunth) Nees, Syst. Laur.: 302. 1836 ≡ *Nectandra sanguinea* var. *lanceolata* Meisn. in Candolle, Prodr. 15(1): 164. 1864 – **Lectotype** (first-step designated by Rohwer in Fl. Neotrop. Monogr. 60: 71. 1993; **second-step, designated here**): Mexico. Guerrero: Acapulco, *Humboldt & Bonpland 3880* (P barcode

- P00128686!; isoelectotypes: B barcode B 10 0243838!, B-W barcode B -W 07815 -01 0!, MICH barcode 1210245 [photo!], P barcodes P00128687! & P00128688!).
- = *Nectandra loesneri* Mez in Bull. Herb. Boissier, sér. 2, 5: 243. 1905 (“*loesnerii*”) – Holotype: Mexico. Veracruz: Between Cazonos and Tuxpan, 4 Jan 1903 (fl, fr imm), *Seler & Seler 3696* (B barcode B 10 0243836!; isotype: B barcode B 10 0243837!).
- = *Nectandra cayoana* Lundell in Wrightia 5: 333–334. 1977 – Holotype: Belize. El Cayo Dist.: 1.5 miles SE of Round Hole Bank, Chiquibul forest reserve, 520 m, 25 Apr 1969 (fl), *Proctor 30073* (LL barcode 00370877 [photo!]; isotypes: BM barcode BM000542718!, MO barcode MO-2204502!).

The spelling of *Nectandra loesneri* is corrected here in accordance with Art. 60.12. and Rec. 60C.1(a) of the *Code* (McNeill & al., 2012).

18. *Damburneya salicina* (C.K.Allen) Trofimov & Rohwer, **comb. nov.** ≡ *Nectandra salicina* C.K.Allen in J. Arnold Arbor. 26: 385. 1945 – Holotype: Costa Rica. Alajuela: Between San Miguel and La Palma de San Ramón, 900–950 m, 7 Feb 1925 (fl), *Brenes 4206 (218)* (F!; isotypes: A barcode 00041907!, NY barcode 00355394 [photo!]; fragments A barcode 00041906!).
- = *Nectandra davidsoniana* C.K.Allen in J. Arnold Arbor. 26: 369–370. 1945 – Holotype: Panama, Chiriquí, Chiquero, Boquete, 11 Apr 1938, *Davidson 564* (A barcode 00041894 [photo!]; isotypes: F barcode v0061454F [photo!], MO barcode MO-217167!, US barcode 00099277!).
- Annotations on the herbarium specimens in F and MO show that both W.C. Burger in 1986 and J.G. Rohwer in 1990 thought that *Nectandra davidsoniana* was a species of *Ocotea*. The new combination, however, was never published. In 2000, H. van der Werff recognized that it was conspecific with *Nectandra salicina*. As both *N. davidsoniana* and *N. salicina* have been published in the same paper, we can choose one of them as the basionym of our new combination. Consequently, we selected the name that is based on better material.
19. *Damburneya smithii* (C.K.Allen) Trofimov & Rohwer, **comb. nov.** ≡ *Nectandra smithii* C.K.Allen in J. Arnold Arbor. 26: 370. 1945 – Holotype: Costa Rica. Alajuela: Region of Zarcero, Zapote de San Carlos, 1600 m, 25 Mar 1938 (fl), *A. Smith H541* (A barcode 00041911 [photo!]; isotypes: F barcode v0061464F!, MO barcode MO-2204489!).

20. *Damburneya umbrosa* (Kunth) Trofimov, **comb. nov.** ≡ *Ocotea umbrosa* Kunth in Humboldt & al., Nov. Gen. Sp. 2: 128 [folio ed.] or 161 [quarto ed.]. 1817 ≡ *Persea umbrosa* (Kunth) Spreng., Syst. Veg. 2: 269. 1825 ≡ *Oreodaphne umbrosa* (Kunth) Nees, Syst. Laur.: 456 [nec ibid. p. 388]. 1836, nom. illeg. ≡ *Oreodaphne humboldtii* Meisn. in Candolle, Prodr. 15(1): 129. 1864, nom. illeg. ≡ *Nectandra umbrosa* (Kunth) Mez in Jahrb. Königl. Bot. Gart. Berlin 5: 462. 1889 – **Lectotype** (first-step designated by Rohwer in Fl. Neotrop. Monogr. 60: 76. 1993; **second-step,**

**designated here):** Without locality (Colombia?), *Humboldt & Bonpland s.n.* (P barcode P00128735!; isolectotypes: B-W barcode B -W 07801 -01 0!, P barcode P00128736!).

In his monograph, Rohwer (1993) attributed also *Nectandra minima* Rohwer to the *N. coriacea* group. We hesitate to transfer this species to *Damburneya* now, because it differs in several characters from the other species and approaches *Ocotea* even more than these. It has smaller, less papillose flowers and stamens with almost superposed pairs of pollen sacs. The most important difference from both *Damburneya* and *Nectandra*, however, is the fact that it sometimes has unisexual flowers. Within the *Ocotea* complex, this condition is known only from *Endlicheria*, *Rhodostemonodaphne*, and many species of *Ocotea*. *Endlicheria* is defined by disporangiate anthers (at least in the two outer androecial whorls), whereas they are tetrasporangiate in *Ocotea* and *Rhodostemonodaphne*. *Rhodostemonodaphne* differs by broadly sessile, fleshy anthers with the pollen sacs arranged in a single apical row. Unfortunately, we have not been able to extract DNA of sufficient quality for amplification from the relatively old herbarium material available of *Nectandra minima*.

## ■ ACKNOWLEDGMENTS

We thank the former curators of HBG, Hans-Helmut Poppendieck and Tassilo Feuerer, for allowing DNA extraction from numerous specimens. Many samples also have been collected by Pedro L.R. de Moraes, Universidade Estadual Paulista, Rio Claro, Brazil, in part during a collecting trip with the senior author of this paper in 2011. Jim Solomon is gratefully acknowledged for providing samples from the Missouri Botanical Garden DNA bank, and H. David Clarke, University of North Carolina at Asheville, for providing samples collected during his time as resident plant collector in Guyana for the Smithsonian Institution (voucher specimens in US). Stephan G. Beck, Herbario Nacional de Bolivia (LPB), La Paz, Bolivia, sent numerous collections to the senior author as gifts for determination. Individual samples were also provided by Maria Baden, Univ. Aarhus, Denmark; Beat Leuenberger, Bot. Gard. Berlin, Germany; Wolfram Lobin, Bot. Gard. Bonn, Germany; Michaela Wernisch, Univ. Vienna, Austria; and Scott Zona, Fairchild Tropical Garden, Miami, U.S.A.

Andrea Jounais and Anna Maria Vogt are gratefully acknowledged for their skilled technical assistance in the lab. We also thank our student assistants, B.Sc., M.Sc. and diploma candidates (Imke Bodendieck, Kolja Dudas, Torsten Hoche, Anja zur Loye, Randi Rohde and Kristina Ruthe) for some sequences of *Aiouea*, *Cinnamomum*, *Ocotea* and *Phoebe*. Henk van der Werff and Pedro Moraes are gratefully acknowledged for their helpful comments on an earlier version of this manuscript.

## ■ LITERATURE CITED

Allen, C.K. 1966. Notes on Lauraceae of tropical America I. The generic status of *Nectandra*, *Ocotea*, and *Pleurothyrium*. *Phytologia* 13: 221–231.  
<http://biodiversitylibrary.org/item/50642#page/227/mode/1up>

- Alvarez López, E. 1955. Comentario sobre “Laurus”, de Ruiz y Pavón, con notas de Dombey acerca de algunas de sus especies. *Anales Inst. Bot. Cavanilles* 13: 71–78.  
<https://dialnet.unirioja.es/descarga/articulo/2977945.pdf>
- Anzótegui, L.M. & Aceñolaza, P.G. 2008. Macrofloristic assemblage of the Paraná Formation (Middle-Upper Miocene) in Entre Ríos (Argentina). *Neues Jahrb. Geol. Paläontol. Abh.* 248: 159–170.  
<http://dx.doi.org/10.1127/0077-7749/2008/0248-0159>
- Aublet, F. 1775. *Histoire des plantes de la Guiane française*, vol. 2. Londres [London] & Paris: chez Pierre-François Didot jeune.  
<http://dx.doi.org/10.5962/bhl.title.674>
- Bentham, G. 1880. Laurineae. Pp. 146–168 in: Bentham G. & Hooker J.D., *Genera plantarum*, vol. 3(1). Londini [London]: venit apud L. Reeve, etc. <http://dx.doi.org/10.5962/bhl.title.747>
- Bernardi, L. 1962. *Lauráceas*. Mérida: Talleres Gráficos Universitarios, Universidad de Los Andes.
- Berry, E.W. 1914. The Upper Cretaceous and Eocene floras of South Carolina and Georgia. *Profess. Pap. U.S. Geol. Surv.* 84: 1–200.
- Berry, E.W. 1922. The flora of the Concepcion-Arauco coal measures of Chile. *Johns Hopkins Univ. Stud. Geol.* 4: 73–143.  
<http://babel.hathitrust.org/cgi/pt?id=njp.32101080318148;view=1up;seq=337>
- Berry, E.W. 1924. The Middle and Upper Eocene floras of southeastern North America. *Profess. Pap. U.S. Geol. Surv.* 92: 1–206.  
<http://pubs.usgs.gov/pp/0092/report.pdf>
- Berry, E.W. 1925. The flora of the Ripley formation. *Profess. Pap. U.S. Geol. Surv.* 136: 1–94. <http://pubs.usgs.gov/pp/0136/report.pdf>
- Berry, E.W. 1931. A flora of Green River age in the Wind River basin of Wyoming. *Profess. Pap. U.S. Geol. Surv.* 165: 55–81.  
<http://pubs.usgs.gov/pp/0165/report.pdf>
- Berry, E.W. 1936. Tertiary plants from Venezuela. *Proc. U. S. Natl. Mus.* 83: 335–360. <http://www.jstor.org/stable/2481054>
- Beyra Matos, A. & Lavin, M. 1999. Monograph of *Pictetia* (Leguminosae-Papilionoideae) and review of the Aeschynomeneae. *Syst. Bot. Monogr.* 56: 1–93. <http://www.jstor.org/stable/25096650>
- Bijl, P.K., Houben, A.J.P., Schouten, S., Bohaty, S.M., Sluijs, A., Reichart, G.-J., Sinninghe Damsté, J.S. & Brinkhuis, H. 2010. Transient Middle Eocene atmospheric CO<sub>2</sub> and temperature variations. *Science* 330: 819–821.  
<http://dx.doi.org/10.1126/science.1193654>
- Bohati, S.M. & Zachos, J.C. 2003. Significant Southern Ocean warming event in the late middle Eocene. *Geology* 31: 1017–1020.  
<http://dx.doi.org/10.1130/G19800.1>
- Britton, N. & Millspaugh, C.F. 1920. *The Bahama flora*. New York: published by the authors. <http://dx.doi.org/10.5962/bhl.title.54084>
- Catesby, M. 1754. *The natural history of Carolina, Florida, and the Bahama Islands*, vol. 2. London: printed for C. Marsh C. and T. Wilcox. <http://dx.doi.org/10.5962/bhl.title.10313>
- Chanderbali, A.S., Van der Werff, H. & Renner, S. 2001. Phylogeny and historical biogeography of Lauraceae: Evidence from the chloroplast and nuclear genomes. *Ann. Missouri Bot. Gard.* 88: 104–134. <http://www.jstor.org/stable/2666133>
- Christophel, D.C., Kerrigan, R. & Rowett, A.I. 1996. The use of cuticular features in the taxonomy of the Lauraceae. *Ann. Missouri Bot. Gard.* 83: 419–432. <http://www.jstor.org/stable/2399871>
- Dong, W., Liu, J., Yu, J., Wang, L. & Zhou, S. 2012. Highly variable chloroplast markers for evaluating plant phylogeny at low taxonomic levels and for DNA barcoding. *PLOS ONE* 7: e35071.  
<http://dx.doi.org/10.1371/journal.pone.0035071>
- Felsenstein, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* 39: 783–791.  
<http://statweb.stanford.edu/~nzhang/Stat366/Felsenstein85.pdf>
- Folguera, A., Orts, D., Spagnuolo, M., Vera, E.R., Litvak, V., Sagripanti, L., Ramos, M.E. & Ramos, V.A. 2011. A review of Late Cretaceous to Quaternary palaeogeography of the southern Andes. *Biol. J. Linn. Soc.* 103: 250–268.
- Gentry, A.H. 1982. Neotropical floristic diversity: Phytogeographical

- connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? *Ann. Missouri Bot. Gard.* 69: 557–593. <http://doi.org/10.2307/2399084>
- Greenwood, D.R. & Wing, S.L.** 1995. Eocene continental climates and latitudinal temperature gradients. *Geology* 23: 1044–1048. [http://dx.doi.org/10.1130/0091-7613\(1995\)023<1044:ECCALT>2.3.CO;2](http://dx.doi.org/10.1130/0091-7613(1995)023<1044:ECCALT>2.3.CO;2)
- Hamann, A. & Wang, T.** 2005. Models of climatic normals for geneecology and climate change studies in British Columbia. *Agric. Forest Meteorol.* 128: 211–221. <http://dx.doi.org/10.1016/j.agrformet.2004.10.004>
- Hamann, A. & Wang, T.** 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. *Ecology* 87: 2773–2786. [http://dx.doi.org/10.1890/0012-9658\(2006\)87\[2773:PEOCCO\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2006)87[2773:PEOCCO]2.0.CO;2)
- Heinze, B.** 2007. A database of PCR primers for the chloroplast genomes of higher plants. *Pl. Meth.* 3: 4. <http://dx.doi.org/10.1186/1746-4811-3-4>
- Hoorn, C., Wesselingh, F.P., Ter Steege, H., Bermudez, M.A., Mora, A., Sevink, J., Sanmartín, I., Sanchez-Meseguer, A., Anderson, C.L., Figueiredo, J.P., Jaramillo, C., Riff, D., Negri, F.R., Hooghiemstra, H., Lundberg, J., Stadler, T., Särkinen, T. & Antonelli, A.** 2010. Amazonia through time: Andean. *Science* 330: 927–931. <http://dx.doi.org/10.1126/science.1194585>
- Howard, R.A.** 1981. Nomenclatural notes on the Lauraceae of the Lesser Antilles. *J. Arnold Arbor.* 62: 45–61. <http://www.biodiversitylibrary.org/item/33625#page/47/mode/1up>
- Howard, R.A. & Staples, G.W.** 1983. The modern names for Catesby's plants. *J. Arnold Arbor.* 64: 511–546. <http://www.biodiversitylibrary.org/item/33627#page/538/mode/1up>
- Huang, J.F., Li, L., Van der Werff, H., Li, H.W., Rohwer, J.G. & Crayn, D.M.** 2016. Origins and evolution of cinnamon and camphor: A phylogenetic and historical biogeographical analysis of the *Cinnamomum* group (Lauraceae). *Molec. Phylogen. Evol.* 96: 33–44. <http://dx.doi.org/10.1016/j.ympev.2015.12.007>
- Huber, M. & Caballero, R.** 2011. The early Eocene equable climate problem revisited. *Clim. Past* 7: 241–304. <http://dx.doi.org/10.5194/cp-7-603-2011>
- Hyland, E.G. & Sheldon, N.** 2013. Coupled CO<sub>2</sub>-climate response during the Early Eocene Climatic Optimum. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 369: 125–135. <http://dx.doi.org/10.1016/j.palaeo.2012.10.011>
- Iturralde-Vinent, M.A. & MacPhee, R.D.E.** 1999. Paleogeography of the Caribbean region: Implications for Cenozoic biogeography. *Bull. Amer. Mus. Nat. Hist.* 238: 1–95. <http://digitallibrary.amnh.org/dspace/bitstream/handle/2246/1642/B238a01.pdf?sequence=2>
- Käss, E. & Wink, M.** 1997. Molecular phylogeny and phylogeography of the genus *Lupinus* (family Leguminosae) inferred from nucleotide sequences of the *rbcL* gene and ITS 1+2 sequences of rDNA. *Pl. Syst. Evol.* 208: 139–167. <http://link.springer.com/article/10.1007/BF00985439>
- Klak, C., Bruyns, P.V. & Hanáček, P.** 2013. A phylogenetic hypothesis for the recently diversified Ruschieae (Aizoaceae) in southern Africa. *Molec. Phylogen. Evol.* 69: 1005–1020. <http://dx.doi.org/10.1016/j.ympev.2013.05.030>
- Klucking, E.P.** 1987. *Leaf venation patterns*, vol. 2, *Lauraceae*. Stuttgart: J. Cramer.
- Kostermans, A.J.G.H.** 1957. Lauraceae. *Commun. Forest Res. Inst., Bogor* 57: 1–64. Reprint available at <http://e-journal.biologi.lipi.go.id/index.php/reinwardtia/article/download/1003/869>
- Kress, W.J., Wurdack, K.J., Zimmer, E.A., Weigt, L.A. & Janzen, D.H.** 2005. Use of DNA barcodes to identify flowering plants. *Proc. Natl. Acad. Sci. U.S.A.* 102: 8369–8374. <http://dx.doi.org/10.1073/pnas.0503123102>
- Kress, W.J., Erickson, D.L., Jones, F.A., Swenson, N.G., Perez, R., Sanjurjo, O. & Bermingham, E.** 2009. Plant DNA barcodes and a community phylogeny of a tropical forest dynamics plot in Panama. *Proc. Natl. Acad. Sci. U.S.A.* 106: 18621–18626. <http://dx.doi.org/10.1073/pnas.0909820106>
- Kvaček, Z.** 1971. Fossil Lauraceae in the stratigraphy of the North-Bohemian Tertiary. *Sborn. Geol. Ved., Paleontol.* 13: 47–86. <https://drive.google.com/file/d/0B4sks78KK5WzSupPU3BjdnZmM0k/view?pref=2&pli=1>
- Lindley, J.** 1836. *A natural system of botany*, ed. 2. London: Longman, etc. [http://reader.digitale-sammlungen.de/de/fs1/object/display/bsb10302245\\_00007.html](http://reader.digitale-sammlungen.de/de/fs1/object/display/bsb10302245_00007.html)
- Liogier, A.H.** 1982. Novitates Antillanae IX. *Phytologia* 50: 161–170. <http://dx.doi.org/10.5962/bhl.part.16099>
- Lorea Hernández, F.G.** 1996. *A systematic revision of the Neotropical species of Cinnamomum Schaeffer (Lauraceae)*. Dissertation, University of Missouri, St. Louis, U.S.A. <http://biodiversitylibrary.org/page/11267032>
- Madrriñán, S.** 2004. *Rhodostemonodaphne* (Lauraceae). *Fl. Neotrop. Monogr.* 92: 1–102.
- McNeill, J., Barrie, F.R., Buck, W.R., Demoulin, V., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Marhold, K., Prado, J., Prud'homme van Reine, W.F., Smith, G.F., Wiersema, J.H. & Turland, N.J. (eds.)** 2012. *International Code of Nomenclature for algae, fungi, and plants (Melbourne Code)*. Regnum Vegetabile 154. Königstein: Koeltz Scientific Books. <http://www.iapt-taxon.org/nomen/main.php>
- Meissner, C.D.F.** 1864. Lauraceae (Ordo 162). Pp. 1–260 in: Candolle, A.L.P.P. de (ed.), *Prodromus systematis universalis regni vegetabilis*, vol. 15. Parisiis [Paris]: Victoris Masson et Filii. <http://dx.doi.org/10.5962/bhl.title.286>
- Michaux, A.** 1803. *Flora boreali-americana*, vol. 1. Parisiis & Argentorati [Paris & Strasbourg]: apud fratres Levrault. <http://dx.doi.org/10.5962/bhl.title.5088>
- Mez, C.C.** 1889. Lauraceae americanae: Monographice descriptis. *Jahrb. Königl. Bot. Gart. Berlin* 5: 1–556. <http://dx.doi.org/10.5962/bhl.title.15443>
- Montes, C., Cardona, A., Jaramillo, C., Pardo, A., Silva, J.C., Valencia, V., Ayala, C., Pérez-Angel, L.C., Rodríguez-Parra, L.A., Ramirez, V. & Niño, H.** 2015. Middle Miocene closure of the Central American seaway. *Science* 348: 225–229. <http://dx.doi.org/10.1126/science.aaa2815>
- Muscarella, R., Uriarte, M., Erickson, D.L., Swenson, N.G., Zimmerman, J.K. & Kress, W.J.** 2014. A well-resolved phylogeny of the trees of Puerto Rico based on DNA barcode sequence data. *PLOS ONE* 9: e112843. <http://dx.doi.org/10.1371/journal.pone.0112843>
- Nees von Esenbeck, C.G.D.** 1833. Revisio laurinarum ab Sellowio in Brasilia collectarum et iam in Herbario Regio Berolinensi asseratarum. *Linnaea* 8: 36–51. <http://emedien3.sub.uni-hamburg.de/han/sfx/www.botanicus.org/page/98929> <http://biodiversitylibrary.org/item/10852#page/39/mode/1up>
- Nees von Esenbeck, C.G.D.** 1836. *Systema laurinarum*. Berolini [Berlin]: sumptibus Veitii et sociorum. <http://dx.doi.org/10.5962/bhl.title.422>
- Nuttall, T.** 1818. *The genera of North American plants, and a catalogue of the species, to the year 1817*. Philadelphia: printed for the author. <http://dx.doi.org/10.5962/bhl.title.290>
- Pennington, R.T. & Dick, C.W.** 2004. The role of immigrants in the assembly of the South American rainforest tree flora. *Philos. Trans., Ser. B* 359: 1611–1622. <http://dx.doi.org/10.1098/rstb.2004.1532>
- Persoon, C.H.** 1805. *Synopsis plantarum*, vol. 1. Parisiis Lutetiorum [Paris]: apud Carol. Frid. Cramerum; Tubingae [Tübingen]: apud J.G. Cottam. <http://bibdigital.rjb.csic.es/ing/Libro.php?Libro=383>
- Rafinesque, C.S.** 1838. *Sylva telluriana*. Philadelphia: printed for the author and publisher. <http://dx.doi.org/10.5962/bhl.title.248>

- Rohwer, J.G. 1986. Prodrum einer Monographie der Gattung *Ocotea* Aubl. (Lauraceae), sensu lato. *Mitt. Inst. Allg. Bot. Hamburg* 20: 3–278.
- Rohwer, J.G. 1991. Borderline cases between *Ocotea*, *Nectandra*, and *Phoebe* (Lauraceae): The “marginal” species of the *Ocotea helicterifolia*-group, including the *O. heydeana* group. *Bot. Jahrb. Syst.* 112: 365–397.
- Rohwer, J.G. 1993. *Flora Neotropica Monographs*, vol. 60, *Lauraceae: Nectandra*. New York: The New York Botanical Garden.
- Rohwer, J.G. 2012. *Nectandra ovatocaudata*, a new species of Lauraceae from Cajamarca, Peru. *Novon* 22: 220–222. <http://dx.doi.org/10.3417/2011099>
- Rohwer, J.G. & Kubitzki, K. 1985. Entwicklungslinien im *Ocotea*-Komplex (Lauraceae). *Bot. Jahrb. Syst.* 107: 129–135.
- Rohwer, J.G. & Rudolph, B. 2005. Jumping genera: The phylogenetic positions of *Cassytha*, *Hypodaphnis*, and *Neocinnamomum* (Lauraceae) based on different analyses of *trnK* intron sequences. *Ann. Missouri Bot. Gard.* 92: 153–178. <http://www.jstor.org/stable/3298512>
- Rohwer, J.G., Li, J., Rudolph, B., Schmidt, S.A., Van der Werff, H. & Li, H.-W. 2009. Is *Persea* (Lauraceae) monophyletic? Evidence from nuclear ribosomal ITS sequences. *Taxon* 58: 1153–1167. <http://www.jstor.org/stable/27757009>
- Rohwer, J.G., Moraes, P.L.R. de, Rudolph, B. & Van der Werff, H. 2014. A phylogenetic analysis of the *Cryptocarya* group (Lauraceae), and relationships of *Dahlgrenodendron*, *Sinopora*, *Triadodaphne*, and *Yasunia*. *Phytotaxa* 158: 111–132. <http://dx.doi.org/10.11646/phytotaxa.158.2.1>
- Ronquist, F., Huelsenbeck, J.P. & Teslenko, M. 2011. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574. <http://dx.doi.org/10.1093/bioinformatics/btg180>
- Sang, T., Crawford, D.J. & Stuessy, T.F. 1997. Chloroplast DNA phylogeny, reticulate evolution, and biogeography of *Paeonia* (Paeoniaceae). *Amer. J. Bot.* 84: 1120–1136. <http://dx.doi.org/10.3732/ajb.94.3.400>
- Savage, J.M. 1982. The enigma of the Central American herpetofauna: Dispersals or vicariance? *Ann. Missouri Bot. Gard.* 69: 464–547. <http://www.jstor.org/stable/2399082>
- Schreber, J.C.D. 1791. *Genera plantarum*, vol. 2. Francofurti ad Moenum [Frankfurt a. M.]: sumtu Varrentrappii et Wenneri. <http://bibdigital.rjb.csic.es/ing/Libro.php?Libro=3975>
- Simmons, M.P. & Ochoterena, H. 2000. Gaps as characters in sequence-based phylogenetic analyses. *Syst. Biol.* 49: 369–381. <http://dx.doi.org/10.1093/sysbio/49.2.369>
- Song, J., Yao, H., Li, Y., Li, X., Lin, Y., Liu, C., Han, J., Xie, C. & Chen, S. 2009. Authentication of the family Polygonaceae in Chinese pharmacopoeia by DNA barcoding technique. *J. Ethnopharmacol.* 124: 434–439. <http://dx.doi.org/10.1016/j.jep.2009.05.042>
- Stafleu, F.A. & Cowan, R.S. 1979. *Taxonomic literature*, ed. 2, vol. 2. Utrecht: Bohn, Scheltema & Holkema; The Hague: W. Junk. <http://dx.doi.org/10.5962/bhl.title.48631>
- Swofford, D.L. 2001. PAUP\*: Phylogenetic analysis using parsimony (\*and other methods), version 4.0b10. Sunderland: Sinauer.
- Tamura, K., Stecher, G., Peterson, D., Filipowski, A. & Kumar, S. 2013. MEGA6: Molecular evolutionary genetics analysis. Version 6.0. *Molec. Biol. Evol.* 30: 2725–2729. <http://dx.doi.org/10.1093/molbev/mst197>
- Tate, J. A. 2002. *Systematics and evolution of Tarasa (Malvaceae): An enigmatic Andean polyploid genus*. Dissertation, The University of Texas at Austin, U.S.A. <https://www.lib.utexas.edu/etd/d/2002/tateja026/tateja026.pdf>
- Van der Werff, H. 1991. A key to the genera of Lauraceae in the New World. *Ann. Missouri Bot. Gard.* 78: 377–387. <http://www.jstor.org/stable/2399567>
- Van der Werff, H. 1999. New taxa and combinations in the *Ocotea helicterifolia* (Lauraceae) species group. *Novon* 9: 571–583. <http://www.jstor.org/stable/3392170>
- White, T.J., Bruns, T., Lee, S. & Taylor, J.W. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Pp. 315–322 in: Innis, M.A., Gelfand, D.H., Sninsky, J.J. & White T.J. (eds.), *PCR protocols: A guide to methods and applications*. New York: Academic Press, Inc.
- Yao, H., Song, J.Y., Ma, X.Y., Liu, C., Xu, H.X., Han, J.P., Duan, L.S. & Chen, S.L. 2009. Identification of *Dendrobium* species by a candidate DNA barcode sequence: The chloroplast *psbA-trnH* intergenic region. *Pl. Med. (Stuttgart)* 75: 667–669. <http://dx.doi.org/10.1055/s-0029-1185385>
- Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292: 686–693. <http://dx.doi.org/10.1126/science.1059412>

#### Appendix 1. Species examined. Taxon, origin, voucher information and GenBank/NCBI accession numbers.

The species of the *Nectandra coriacea* group are listed under *Damburneya*, to which they have been transferred at the end of the paper. Designations in parentheses refer to Lorea Hernández (1996) and have not yet been validly published. Accession numbers beginning with AF are from Chanderbali & al. (2001); with EU from Madriñán & Chacon (unpub.); with GQ4 from Assis & Mello-Silva (unpub.); with GQ9 from Kress & al. (2009); with FM from Rohwer & al. (2009); with KJ from Muscarella & al. (2014); numbers beginning with KX are new sequences, the first number is the sequence of the chloroplast *psbA-trnH* spacer and the second number the nuclear ITS sequence.

*Actinodaphne sesquipedalis* Meisn., Malaysia, Kuala Lumpur, *Saw Leng Guan s.n.* (KEP), AF268787, AF272247; *Aiouea guianensis* Aubl., Guyana, Demerara, *Taylor 12085* (MO), AF268780, AF272251; *A. saligna* Meisn., Brazil, Espírito Santo, 5 Sep 2011, *Moraes 3165* (HBG), KX509821, KX509881; *Aniba cinnamomiflora* C.K.Allen, Venezuela, Trujillo, *Cuello 955* (MO), AF268770, AF272254; *Cinnamomum camphora* (L.) J.Presl, Germany, Hamburg Bot. Gard., 23 Jan 2013, *Rohwer s.n.* (HBG), KX509822, KX509882; *C. formicarium* van der Werff & Lorea-Hern., Ecuador, Bolívar, 10 Jul 1991, *Van der Werff 12498* (HBG), KX509823, KX509883; (“*C. hirsutum* Lorea-Hern.”), Brazil, São Paulo, 25 Aug 2011, *Moraes s.n.* (HRCB), KX509824, KX509884; *C. japonicum* Siebold, #1: Germany, Berlin Bot. Gard., Jan 2002, *Leuenerberger s.n.* (HBG), KX509825; #2: Germany, Hamburg Bot. Gard., 10 Jan 2013, *Rohwer s.n.* (HBG), KX509885; *C. “pseudoglaziovii”* Lorea-Hern., Brazil, São Paulo, 23 Jan 2013, *Moraes 3344* (HRCB), KX509826, KX509886; *C. verum* J.Presl, Germany, Bonn Bot. Gard., 29 Sep 2010, *Lobin 19349* (HBG), KX509827, KX509887; *Damburneya (Nectandra) ambigens* (S.F.Blake) Trofimov, Mexico, Veracruz-Oaxaca, 15 Feb 1981, *Wendt 3190* (HBG), KX509828, KX509888; *D. (Nectandra) coriacea* (Sw.) Trofimov & Rohwer, U.S.A., Fairchild Trop. Gard., 8 Oct 1997, *Zona s.n.* (HBG), KX509829, KX509889; *D. gentlei* (Lundell) Trofimov ≡ *Nectandra lundellii* C.K.Allen, Mexico, Veracruz-Oaxaca, 25 Mar 1981, *Wendt 3060* (HBG), KX509830, KX509890; *D. (Nectandra) martinicensis* (Mez) Trofimov, Belize, Cayo, 4 Jul 2006, *Vandrot 123* (HBG), KX509831, KX509891; *D. (Nectandra) patens* (Sw.) Trofimov, Jamaica, Surrey, 6 Nov 1980, *Kapos 1584* (HBG), KX509832, KX509892; *D. (Nectandra) purpurea* (Ruiz & Pav.) Trofimov, #1: Peru, Cajamarca, *Campos 3165* (MO), AF272293; #2: Panama, *BCI 415163* (ANDES), EU153974; *D. (Nectandra) salicifolia* (Kunth) Trofimov & Rohwer, #1: Costa Rica, *Gomez-Laurito s.n.* (unknown), AF272294; #2: Belize, without locality and date, *Baden 977\*1* (HBG), KX509893; *Dicypellium manauseense* W.A.Rodrigues, Brazil, Amazonas, *Assunção & Pereira 749* (MO), AF268775, AF272270; *Endlicheria chalisea* Chanderb., Guyana, Essequibo, *Chanderbali 252* (MO), AF268756, AF272271; *Kubitzkia mezii* (Kosterm.) van der Werff, Guyana, Essequibo, *Chanderbali 249* (MO), AF268772, AF272276; *Laurus nobilis* L., U.S.A., St. Louis, Missouri Bot. Gard., *Chanderbali 327* (MO), AF268785, AF272278; *Licaria cannella* (Meisn.) Kosterm., Guyana,

## Appendix 1. Continued.

Demerara, *Chanderbali 234* (MO), AF268773, AF272280; **L. triandra** (Sw.) Kosterm., U.S.A., Florida, Fairchild Trop. Gard., *Qiu 90019* (NCU), AF268774, AF272282; **Lindera benzoin** (L.) Blume, U.S.A., Missouri Bot. Gard., *Chanderbali 324* (MO), AF268788, AF272283; **Machilus grijsii** Hance, Germany, Hamburg Bot. Gard., 23 Jan 2013, *Rohwer 193* (HBG), KX509833, FM957810; **Nectandra acutifolia** (Ruiz & Pav.) Mez, Bolivia, La Paz, 9 Oct 2001, *Beck 28334* (HBG), KX509834, KX509894; **N. amazonum** Nees, #1: Germany, Hamburg Bot. Gard., *Rohwer s.n.* (HBG), FM957816; #2: Bolivia, Beni, 30 Nov 1998, *Maldonado 115* (HBG), KX509895; **N. 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. canescens** Nees & Mart., Brazil, Amazonas, 19 Feb 1977, *Prance 24476* (HBG), KX509838, KX509899; **N. citrifolia** Mez & Rusby, Ecuador, Esmeraldas, 12 Feb 1996, *Clark 2065* (HBG), KX509842, KX509902; **N. cuneatocordata** Mez, Bolivia, Pando, 18 Sep 1983, *Solomon 10870* (HBG), KX509843, KX509903; **N. cuspidata** Nees & Mart. ex Nees, #1: Brazil, *Assis 1151* (SPF), GQ480369; #2: without locality, *FC 1579* (ANDES), EU153966; **N. discolor** (Kunth) Nees, Peru, Amazonas, 29 Aug 1998, *Vasquez 25328* (HBG), KX509844, KX509904; **N. grandiflora** Nees & Mart., Brazil, São Paulo, 3 Jun 2011, *Moraes 3148* (HBG), KX509845, KX509905; **N. herrerae** O.C.Schmidt, Peru, Cusco, 29 Nov 2002, *Calatayud 1235* (HBG), KX509846, KX509906; **N. hihua** (Ruiz & Pav.) Rohwer, Cuba, Holguín, 3 May 1980, *Álvarez de Zayas 42637* (JE), KX509847, KX509907; **N. lanceolata** Nees & Mart. ex Nees, #1: without locality, *Assis 937* (CESJ, SPF), GQ480370; #2: Paraguay, Alto Parana, 9 Nov 1995, *Schimini 29955* (HBG), KX509908; **N. latissima** Rohwer, Bolivia, Beni, 20 Sep 1997, *Mueller 6240* (HBG), KX509848, KX509909; **N. laurel** Klotzsch ex Nees, Peru, Pasco, 30 Oct 2009, *Rojas 7105* (HGB), KX509849, KX509910; **N. leucantha** Nees & Mart., Brazil, Paraná, 26 May 1989, *Hatschbach 53112* (HBG), KX509850, KX509911; **N. cf. lineata** (Kunth) Rohwer, #1: Peru, Amazonas, 1 Nov 2012, *Van der Werff 24827* (HBG), KX509839; #2: Panama, Barro Colorado Island, 2007, *Perez BCI 441778* (STRI, US), GQ982298; **N. lineatifolia** (Ruiz & Pav.) Mez, Bolivia, La Paz, 7 Aug 2003, *Beck 28963* (HBG), KX509851, KX509912; **N. longifolia** (Ruiz & Pav.) Nees, Bolivia, La Paz, 25 Sep 1991, *Seidel 5346* (HBG), KX509852, KX509913; **N. lundellii** C.K.Allen, see *Damburneya gentlei* (Lundell) Trofimov; **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. cf. megapotamica** (Spreng.) Mez, Brazil, Bahia, 12 Sep 2011, *Moraes 3146* (HRCB), KX509841, KX509901; **N. membranacea** (Sw.) Griseb., Brazil, Espírito Santo, 10 Sep 2011, *Moraes 3222* (HRCB), KX509854, KX509915; **N. micranthera** Rohwer, Brazil, Bahia, 2 Mar 1978, *Mori 9358* (HBG), KX509855, KX509916; **N. microcarpa** Meisn., Peru, San Martín, 10 Aug 1977, *Schunke 9789* (HBG), KX509856, KX509917; **N. nitidula** Nees & Mart., Brazil, Bahia, 4 Dec 2010, *Moraes 3137* (HBG), KX509857, KX509918; **N. obtusata** Rohwer, Ecuador, Pichincha, 11 Jul 1991, *Van der Werff 12296* (HBG), KX509858, KX509919; **N. olida** Rohwer, Peru, Amazonas, 5 Nov 2012, *Van der Werff 25083* (HBG), KX509859, KX509920; **N. oppositifolia** Nees & Mart. ex Nees, Brazil, Bahia, 16 Mar 2009, *Moraes 2597* (HBG), KX509860, KX509921; **N. paranaensis** Coe-Teix., Brazil, São Paulo, 1 Sep 2011, *Moraes 3354* (HRCB), KX509861, KX509922; **N. paucinervia** Coe-Teix., Brazil, Acre, 13 Jun 1981, *Elias de Paula 1464* (HBG), KX509862, KX509923; **N. psammophila** Nees & Mart., #1: Brazil, São Paulo, *Lorea-Hernández 5595* (MO), AF272292; #2: Brazil, Espírito Santo, 15 Dec 2012, *Moraes 3540* (HBG), KX509924; **N. puberula** (Schott) Nees, Brazil, Minas Gerais, 5 Feb 2013, *Moraes 3567* (HRCB), KX509863, KX509925; **N. pulverulenta** Nees, Bolivia, La Paz, 7 Sep 2000, *Cahuaya 48* (HBG), KX509864, KX509926; **N. reflexa** Rohwer, Peru, Pasco, 30 Dec 2012, *Rojas 8831* (HBG), KX509865, KX509927; **N. reticulata** (Ruiz & Pav.) Mez, #1: without locality, *Fiaschi 2532* (CEPEC, SPF), GQ480373; #2: Brazil, Minas Gerais, 22 Dec 2012, *Moraes 3560* (HBG), KX509928; **N. turbacensis** (Kunth) Nees, Puerto Rico, Rio Grande, *Taylor 11746* (MO), AF272295; #2: Panama, *BCI 415163* (ANDES), EU153974; **Neolitsea sericea** (Blume) Koidz., Japan, Honshu, *Yasuda 1355* (MO), AF268792, AF272296; **Ocotea aciphylla** (Nees) Mez, #1: Brazil, Espírito Santo, 9 Sep 2011, *Moraes 3205* (HRCB), KX509866; #2: Brazil, Espírito Santo, 9 Sep 2011, *Moraes 3210* (HRCB), KX509929; **N. botrantha** Rohwer, Guatemala, Quetzaltenango, 21 Apr 2013, *Wernisch s.n.* (HBG), KX509867, KX509930; **O. bullata** (Burch.) E.Mey., South Africa, Natal, *Abbot 6208* (MO), AF267778, AF272298; **O. cf. floribunda** (Sw.) Mez, Brazil, Espírito Santo, 12 Sep 2011, *Moraes 3257* (HRCB), KX509868, KX509931; **O. foetens** (Aiton) Baill., #1: Spain, Tenerife, 10 Mar 2005, *Rohwer 5* (HBG), KX509869; #2: Portugal, Madeira, *Maas 8642* (MO), AF272300; **O. guianensis** Aubl., Guyana, Demerara, *Chanderbali 232* (MO), AF268762, AF272302; **O. macrophylla** Kunth, Ecuador, Carchi, 30 Jul 1989, *Van der Werff 10772* (HBG), KX509870, KX509932; **N. malcomberi** van der Werff, Madagascar, Toliara, 17–20 Oct 1992, *Van der Werff 12576* (MO), AF268779, AF272307; **O. odorifera** (Vell.) Rohwer, Brazil, São Paulo, without date, *Moraes s.n.* (HRCB), KX509871, KX509930; **O. praetermissa** van der Werff, Costa Rica, Cartago, 7 Mar 1987, *Burger 12065* (HBG), KX509872, KX509934; **O. pulchella** (Nees) 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. quixos** (Lam.) Kosterm., Ecuador, Napo, 23 Nov 1990, *Neill 9487* (MO), AF261999, KX509937; **O. salvadorensis** (Lundell) van der Werff, El Salvador, Santa Ana, 25 Sep 1988, *Reyna 1414* (HBG), KX509875, KX509938; **O. sinuata** (Mez) Rohwer, Costa Rica, San José, 8 Mar 1987, *Burger 12086* (HBG), KX509876, KX509939; **Persea americana** Mill., Germany, Hamburg Bot. Gard., 16 Oct 2003, *Rohwer s.n.* (HBG), KX509877, FM957821; **Phoebe shearerii** (Hemsl.) Gamble, Germany, Hamburg Bot. Gard., 7 Jan 2014, *Rohwer s.n.* (HBG), KX509878, KX509940; **Pleurothyrium cinereum** van der Werff, Peru, San Martín, *Van der Werff 15325* (MO), AF268769, AF272339; **P. 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; **Rhodostemonodaphne crenaticupula** Madriñán, Guyana, Essequibo, *Chanderbali 265* (MO), AF268759, AF272331; **Rh. praeclara** (Sandwith) Madriñán, Guyana, Essequibo, *Chanderbali 256* (MO), AF268760, AF272332; **Umbellularia californica** (Hook. & Arn.) Nutt., U.S.A., Missouri Bot. Gard., *Chanderbali 326* (MO), AF268777, AF272337.