



A phylogenetic analysis of the *Cryptocarya* group (Lauraceae), and relationships of *Dahlgrenodendron*, *Sinopora*, *Triadodaphne*, and *Yasunia*

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Abstract

A phylogenetic analysis based on nuclear ITS and plastid *trnK* intron sequences confirms that *Dahlgrenodendron*, *Sinopora*, *Triadodaphne*, and *Yasunia* are members of the *Cryptocarya* group, as expected from morphology. *Dahlgrenodendron* from South Africa is sister to *Aspidostemon* from Madagascar. *Triadodaphne inaequitapala* is nested within *Endiandra* (both from Australasia), and *Yasunia* from South America is nested among South American *Beilschmiedia* species. *Sinopora* is a member of the *Beilschmiedia* clade, but its precise position is still uncertain. Among large genera of the group, *Cryptocarya* is clearly monophyletic, and *Endiandra* appears to be as well, if *T. inaequitapala* is included. *Beilschmiedia* is paraphyletic with respect to (at least) *Potameia* and *Yasunia*. Most well-supported clades within genera are geographically homogeneous, except a clade including the Chilean *Cryptocarya alba* and two New Caledonian species. Both *Beilschmiedia* and *Cryptocarya* have reached the Americas more than once. Four-locular anthers are plesiomorphic in the *Cryptocarya* group; two-locular anthers have arisen by fusion of the two pollen sacs of a theca. In the plesiomorphic fruit type, the ovary is completely enclosed in receptacular tissue; a superior fruit, seated free on its pedicel, is a synapomorphy of the *Beilschmiedia* clade.

Key words: Biogeography, evolution, floral morphology

Introduction

Lauraceae are among the larger families of Magnoliidae and one of the most common families in moist tropical and subtropical forests of the Americas, Asia, and Australia (Gentry 1988). As discussed in more detail by Rohwer (1993) and van der Werff & Richter (1996), morphology-based systems of the family have been divergent, depending on the relative importance attributed to characters by different authors. Molecular studies, in contrast, have been largely congruent and thus have led to a widespread agreement about the major phylogenetic divisions (Rohwer 2000; Chanderbali *et al.* 2001; Rohwer & Rudolph 2005). In these studies, the *Cryptocarya* group, which had first been recognized based on wood and bark anatomy by Richter (1981), turned out to be sister to the rest of the family except *Hypodaphnis* Stapf (1909). The group has been shown to include at least the genera *Beilschmiedia* Nees (1831: 61, 69), *Cryptocarya* Brown (1810: 402), *Endiandra* Brown (1810: 402), *Aspidostemon* Rohwer & Richter (1987: 71), *Potameia* Du Petit-Thouars (1806: 5), *Eusideroxylon* Teijsmann & Binnendijk (1863: 292), and *Potoxylon* Kostermans (1978: 143). *Beilschmiedia* and *Cryptocarya* are species-rich genera, widespread in tropical and subtropical regions of all continents, though estimates of 250 and 350 spp., respectively, by Rohwer (1993) may be too high. *Endiandra* (ca. 100 spp.) is distributed from the Malesian region through eastern Australia to the western Pacific islands. *Potameia* (ca. 25 spp.) has most of its species in Madagascar but has also been reported from India to Southeast Asia, where delimitation from *Syndiclis* Hooker (1886a: pl. 1515)

(ca. 10 spp.) is not entirely clear. *Aspidostemon* (28 spp., van der Werff 2006) is a Malagasy endemic, whereas *Eusideroxylon* and *Potoxylon* are monotypic endemics of the Greater Sunda Islands.

Based on morphology, *Aspidostemon*, *Eusideroxylon*, *Potoxylon* and *Cryptocarya* (including *Ravensara* Sonnerat [1782: 226, plate 127], see van der Werff 1992) appear to be well defined, even though the diversity within *Cryptocarya* led Rohwer (1993) to append the statement “In need of a comprehensive revision, perhaps not monophyletic” to his description. Delimitation of the remaining genera is less straightforward, as has been discussed by Hyland (1989) and van der Werff & Nishida (2010).

Several minor genera of Lauraceae remained unstudied with molecular methods so far, due to lack of suitable material: *Brassiodendron* Allen (1942: 153), *Cinnadenia* Kostermans (1973: 223), *Dahlgrenodendron* van der Merwe & van Wyk in van der Merwe *et al.* (1988: 80), *Dodecadenia* Nees (1831: 61, 63), *Gamanthera* van der Werff & Endress (1991: 401), *Hexapora* Hooker (1886b: 189), *Phyllostemonodaphne* Kostermans (1936: 754), *Syndiclis*, *Triadodaphne* Kostermans (1974a: 119); others have been described after the molecular studies cited above were published: *Sinopora* J. Li, N.H. Xia & H.W. Li (2008: 199), *Yasunia* van der Werff & Nishida (2010: 494). Among these, *Triadodaphne* had been placed in the *Cryptocarya* group based on wood anatomical evidence by Richter (1981) or even in synonymy of *Endiandra* by Rohwer (1993) based on morphology. Rohwer (1993) also placed *Cassytha*, *Dahlgrenodendron*, and *Hypodaphnis* in the *Cryptocarya* group based on fruits in which the ovary is completely surrounded by receptacular tissue. Molecular studies have later shown that *Cassytha* does not belong to this clade and that *Hypodaphnis* is sister to all other Lauraceae (Rohwer 2000; Chanderbali *et al.* 2001; Rohwer & Rudolph 2005). Rohwer (1993) placed *Brassiodendron*, *Hexapora* and *Syndiclis* (the latter as a synonym of *Potameia*) in his *Beilschmiedia* group, which is now part of the *Cryptocarya* group according to the molecular studies cited above. *Gamanthera* and *Phyllostemonodaphne* were placed in the *Aniba* subgroup of the *Ocotea* group by Rohwer (1993), whereas *Dodecadenia* was placed in Laureae. *Cinnadenia* was left as *incertae sedis*. Placement of *Dodecadenia* was confirmed by a molecular analysis of Li *et al.* (2004), but the others are still awaiting study.

Recently, suitable material has become available of *Dahlgrenodendron*, *Sinopora*, and *Yasunia*, and we managed to extract DNA from an older collection of *Triadodaphne inaequitepala* (Kostermans 1969: 485) Kostermans (1993: 131). Based on sequences of the plastid *trnK* intron (including the *matK* gene) and the internal transcribed spacer region of nuclear ribosomal DNA (nrITS), we therefore attempt to answer the following questions. (1) Are *Dahlgrenodendron*, *Sinopora*, and *Yasunia* really members of the *Cryptocarya* group, as has been expected from morphology? (2) Is *Triadodaphne inaequitepala* a species of *Endiandra*, as suggested by van der Werff (2001)? (3) Are the large genera *Beilschmiedia*, *Cryptocarya* and *Endiandra* monophyletic? In addition, we discuss evolution of some key characters in Lauraceae and some disjunctions within the *Cryptocarya* group.

Materials and Methods

Taxon sampling and choice of outgroup.—Samples of plant material were obtained from sources listed in Table 1. In each case, correctness or at least plausibility of the determination was verified, as far as that was possible, often in the absence of recent monographs. BLAST searches showed that all *trnK* intron sequences of the newly investigated genera were most similar to members of the *Cryptocarya* group in the sense of Rohwer (2000) or Cryptocaryae in the sense of Chanderbali *et al.* (2001). In the case of the widespread genera *Beilschmiedia* and *Cryptocarya*, care was taken to include samples from different parts of their range. Based on results of previous molecular studies (Rohwer 2000; Chanderbali *et al.* 2001; Rohwer & Rudolph 2005), *Hypodaphnis zenkeri* (Engler 1899: 385) Stapf (1909: 185) was chosen as outgroup for all analyses. In total, we examined 139 collections of 92 species. In the phylogenetic analysis, however, the number of terminal taxa was reduced to 64, for reasons outlined below.

Molecular methods.—The methods of DNA extraction and amplification have been described in detail by Rohwer & Rudolph (2005) for the *trnK* intron and by Rohwer *et al.* (2009) for the ITS region. These protocols were modified and adjusted to the 3500 Genetic Analyzer sequencing system (Applied Biosystems) as follows. In addition to the primers used in those studies, we designed a new one for each of the sequence regions. The new *trnK* intron primer v510-R (5'-CRA TCA CTC TTT TGA CTT TGG-3') aligns approximately 510 bp downstream from the universal primer 3914-F of Steele & Vilgalys (1994) or about 80 bp downstream from a poly-T region present in almost all Lauraceae. The new primer ITS-H-R (5'-CGG TTC GCT CGC CGT TAC TA-3') was

designed after we found that the primer ITS-26-R of Käss & Wink (1997) has three mismatches for most members of the *Cryptocarya* group. The 5'-end of the new primer overlaps by 10 bp with the 3'-end of the ITS-26 primer. The PCR products were purified either using spin columns of the Montage PCR Filter Units (Millipore) or by degradation of single stranded DNA and proteins with FastAP™ thermosensitive alkaline phosphatase and exonuclease I (Thermo Scientific), both according to manufacturers' instructions. Depending on the amount of pure PCR product, 1:2 to 1:20 dilutions of the PCR product were used for sequencing. The sequencing reactions of the *trnK* intron and ITS region were carried out as described in Rohwer & Rudolph (2005) and Rohwer *et al.* (2009), respectively. The 10 µL sequencing products were precipitated in a mix of 1 µL 125 mM EDTA, 1 µL 3 M sodium acetate, and 25 µL ethanol absolute at room temperature for 20 min, with subsequent centrifugation at 13,000 rpm (ca. 16,600 g) and 4° C for 1 h. The pellet was washed in 35 µL 76% cold ethanol, dried and resuspended in 20 µL HiDi formamide for sequencing analysis using a 3500 Genetic Analyzer capillary sequencer (Applied Biosystems) according to manufacturer's instructions.

The ITS and *trnK* intron sequences of each taxon were confirmed by forward and reverse sequencing reactions, except in a few cases where we had already several confirmed sequences from the same taxon or closely related taxa, so that sequencing in one direction appeared sufficient.

Sequence alignment.—The sequence fragments of each taxon were first edited individually, then aligned automatically using Sequencher™ (GeneCodes), and subsequently checked manually in order to remove any uncertainties. The edited sequences (132 new sequences from this study) have been deposited in EMBL under the accession numbers indicated in Table 1. Sequences in which the accession number starts with HG31 (i.e., all ITS sequences and most *trnK* intron sequences) have been prepared for this study, whereas those starting with AJ247 and AJ627 are from an earlier study (Rohwer & Rudolph 2005).

TABLE 1. Material examined. Sequences with accession numbers starting with HG31 have been prepared for this study, those starting with AJ247 and AJ627 have been prepared for an earlier study (Rohwer & Rudolph 2005).

species	voucher	date of coll.	provenance	acc. no. trnK	acc. no. ITS
<i>Aspidostemon parvifolium</i> (Scott-Elliott 1891: 45) van der Werff (2006: 37)	Lowry 5024 (MO)	13 Mar 1998	Madagascar	AJ627912	HG315527
<i>Beilschmiedia alloiophylla</i> (Rusby 1920: 21) Kostermans (1938: 849)	Yasuda 1308 (MO)	09 Mar 1996	Costa Rica	HG314955	HG315528
<i>Beilschmiedia berteroa</i> (Gay 1849: 301) Kostermans (1938: 858)	Zöllner 21411 (HBG)	12 Feb 1996	Chile	AJ247147	HG315529
<i>Beilschmiedia brenesii</i> Allen (1945: 415)	van der Werff 14015 (MO)	01 Aug 1996	Costa Rica	AJ627914	HG315530
<i>Beilschmiedia brenesii</i>	Yasuda 1314 (MO)	10 Mar 1996	Costa Rica	–	HG315531
<i>Beilschmiedia costaricensis</i> (Mez & Pittier in Mez 1903: 228) Allen (1945: 415)	Yasuda 1309 (MO)	09 Mar 1996	Costa Rica	HG314956	HG315532
<i>Beilschmiedia dictyoneura</i> Kostermans (1965: 24)	Ambri W698 (L)	02 Apr 1991	Indonesia, Kalimantan	HG314957	HG315533
<i>Beilschmiedia emarginata</i> (Meissner 1864: 76) Kostermans (1938: 855)	Moraes s.n. (HRCB)	25 Aug 2011	Brazil, São Paulo	HG314958	HG315534
<i>Beilschmiedia immersinervis</i> Nishida (1999: 678)	Yasuda 1312 (MO)	10 Mar 1996	Costa Rica	HG314959	HG315535
<i>Beilschmiedia madagascariensis</i> (Baillon 1884: 434) Kostermans (1952: 115)	Lowry 5015 (MO)	11 Mar 1998	Madagascar	AJ627915	HG315536
<i>Beilschmiedia mexicana</i> (Mez 1889: 20) Kostermans (1938: 846)	Reyna 1404 (HBG)	25 Sep 1988	El Salvador	AJ247148	HG315537

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TABLE 1 (continued)

species	voucher	date of coll.	provenance	acc. no. trnK	acc. no. ITS
<i>Beilschmiedia miersii</i> (Gay 1849: 298) Kostermans (1938: 860)	<i>Greissl 657-99</i> (MJG)	26 Mar 1999	Chile	AJ627916	HG315538
<i>Beilschmiedia oreophila</i> Schlechter (1906: 107)	<i>McPherson 19086</i> (MO)	30 Oct 2003	New Caledonia	HG314960	HG315539
<i>Beilschmiedia pierreana</i> Robyns & Wilczek (1950: 209)	<i>SIMAB 12418</i> (MO)	Apr 2004	Gabon	HG314961	HG315540
<i>Beilschmiedia recurva</i> Hyland (1989: 155)	<i>van der Werff 17047</i> (MO)	30 Aug 2001	Australia	HG314962	HG315541
<i>Beilschmiedia</i> cf. <i>rigida</i> (Mez 1893: 519) Kostermans (1938: 856)	<i>Moraes 3207</i> (HRCB)	09 Sep 2011	Brazil, Espirito Santo	HG314963	HG315542
<i>Beilschmiedia roxburghiana</i> Nees (1831: 69)	<i>Gerlach s.n.</i> (M)	15 Jul 1997	BG Munich [Nepal to S China, Thailand]	AJ247149	HG315543
<i>Beilschmiedia</i> sp.	<i>Breteler 5283</i> (L)	22 Jul 1968	Cote d'Ivoire	HG314964	HG315544
<i>Beilschmiedia</i> sp.	<i>van der Werff 14189</i> (MO)	01 Apr 1997	Vietnam	HG314965	HG315545
<i>Beilschmiedia</i> sp.	<i>van der Werff 14272</i> (MO)	08 Apr 1997	Vietnam	HG314966	HG315546
<i>Beilschmiedia</i> sp.	<i>van der Werff 17396</i> (MO)	17 Jul 2002	Vietnam	HG314967	HG315547
<i>Beilschmiedia tarairi</i> (Cunningham 1838: 379) Kirk (1889: 71)	<i>Sykes 437511</i> (CHR)	28 Nov 1986	New Zealand	HG314968	HG315548
<i>Beilschmiedia tarairi</i>	<i>Sykes 529799 A</i> (CHR)	02 Dec 1997	New Zealand	HG314969	HG315549
<i>Beilschmiedia tawa</i> (Cunningham 1838: 379) Kirk (1889: 257)	<i>Chase 5519</i> (K)	20 Nov 1997	BG Kew [New Zealand]	AJ247150	–
<i>Beilschmiedia tawa</i>	<i>Dawson</i> (CHR 565486A)	01 Dec 2002	New Zealand	–	HG315550
<i>Beilschmiedia tawa</i>	<i>Heenan</i> (CHR 512618)	10 Jun 1997	New Zealand	HG314970	–
<i>Beilschmiedia tawaroa</i> Wright (1984: 119)	<i>Beever 89046</i> (CHR 450080)	26 Jan 1990	New Zealand	HG314971	HG315551
<i>Beilschmiedia tawaroa</i>	<i>Sykes 221/92</i> (CHR 480004)	27 Nov 1992	New Zealand	HG314972	–
<i>Beilschmiedia tawaroa</i>	<i>Wright 11490</i> (CHR 451260)	26 Apr 1991	New Zealand	HG314973	–
<i>Beilschmiedia tooram</i> (Bailey 1901: 1308) Hyland (1989: 156)	<i>van der Werff 17051</i> (MO)	30 Aug 2001	Australia	HG314974	HG315552
<i>Beilschmiedia velutina</i> (Kostermans 1939: 69) Kostermans (1952: 115)	<i>Razafimandimbison 361</i> (MO)	02 Jul 1998	Madagascar	HG314975	HG315553
<i>Beilschmiedia volckii</i> Hyland (1989: 156)	<i>van der Werff 17052</i> (MO)	30 Aug 2001	Australia	HG314976	HG315554
<i>Cryptocarya alba</i> (Molina 1782: 185, 350) Looser (1950: 65)	<i>Chase 5521</i> (K)	20 Nov 1997	BG Kew [Chile]	AJ247158	–
<i>Cryptocarya alba</i>	<i>Gerlach 95-1146</i> (M)	Nov 2010	BG Munich [Chile]	–	HG315555
<i>Cryptocarya angulata</i> White (1933: 33)	<i>van der Werff 17056</i> (MO)	30 Aug 2001	Australia	HG314977	HG315556
<i>Cryptocarya</i> aff. <i>aschersoniana</i> Mez (1889: 11)	<i>Moraes 2620</i> (HRCB)	02 Apr 2009	Brazil, Espirito Santo	–	HG315557
<i>Cryptocarya</i> aff. <i>aschersoniana</i>	<i>Moraes 2620a</i> (HRCB)	02 Apr 2009	Brazil, Espirito Santo	HG314978	HG315558
<i>Cryptocarya</i> aff. <i>aschersoniana</i>	<i>Moraes 3242</i> (HRCB)	11 Sep 2011	Brazil, Espirito Santo	HG314979	–

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TABLE 1 (continued)

species	voucher	date of coll.	provenance	acc. no. trnK	acc. no. ITS
<i>Cryptocarya bidwillii</i> Meissner (1864: 74)	<i>Grimshaw 2406</i> (L)	29 May 1996	Australia	HG314980	HG315559
<i>Cryptocarya botelhensis</i> Moraes (2007: 51)	<i>Moraes 2311</i> (ESA)	19 Dec 2000	Brazil, São Paulo	HG314981	HG315560
<i>Cryptocarya botelhensis</i>	<i>Moraes 3349</i> (HRCB)	02 Sep 2011	Brazil, São Paulo	HG314982	HG315561
<i>Cryptocarya citriformis</i> (Vellozo 1829: 251) Moraes (2005: 791)	<i>Moraes 3199</i> (HRCB)	08 Sep 2011	Brazil, Espírito Santo	HG314983	HG315562
<i>Cryptocarya cf. citriformis</i>	<i>Moraes 3246</i> (HRCB)	11 Sep 2011	Brazil, Espírito Santo	HG314984	HG315563
<i>Cryptocarya concinna</i> Hance (1882: 79)	<i>Lauerer 70518</i> (UBT)	11 Oct 2010	BG Bayreuth [China]	HG314985	HG315564
<i>Cryptocarya densiflora</i> Blume (1825: 556)	<i>Kinsun Bakia 428</i> (K)	n/a	Malaysia, Borneo	HG314986	HG315565
<i>Cryptocarya gracilis</i> Schlechter (1906: 109)	<i>McPherson 19129</i> (MO)	01 Nov 2003	New Caledonia	HG314987	HG315566
<i>Cryptocarya guillauminii</i> Kostermans (1961: 395)	<i>McPherson 18027</i> (MO)	28 Mar 2001	New Caledonia	HG314988	HG315567
<i>Cryptocarya mandioccana</i> Meissner (1864: 75)	<i>Moraes 31</i> (ESA)	23 Mar 1990	Brazil, São Paulo	HG314989	HG315568
<i>Cryptocarya mandioccana</i>	<i>Moraes 509</i> (ESA)	07 Oct 1991	Brazil, São Paulo	–	HG315569
<i>Cryptocarya mandioccana</i>	<i>Moraes 1245</i> (ESA)	13 Jan 1996	Brazil, São Paulo	–	HG315570
<i>Cryptocarya mannii</i> Hillebrand (1888: 382)	<i>Tangalin 2915</i> (PTBG)	07 Dec 2011	U.S.A., Hawaii	–	HG315571
<i>Cryptocarya mannii</i>	<i>Tangalin 2916</i> (PTBG)	07 Dec 2011	U.S.A., Hawaii	–	HG315572
<i>Cryptocarya mannii</i>	<i>Tangalin 2918</i> (PTBG)	07 Dec 2011	U.S.A., Hawaii	HG314990	HG315573
<i>Cryptocarya mannii</i>	<i>Tangalin 2974</i> (PTBG)	02 Feb 2012	U.S.A., Hawaii	–	HG315574
<i>Cryptocarya mannii</i>	<i>Tangalin 3104</i> (PTBG)	19 Apr 2012	U.S.A., Hawaii	–	HG315575
<i>Cryptocarya mannii</i>	<i>Tangalin 3274</i> (PTBG)	16 Aug 2012	U.S.A., Hawaii	–	HG315576
<i>Cryptocarya mannii</i>	<i>van Balgooy 4206</i> (L)	31 May 1982	U.S.A., Hawaii	–	HG315577
<i>Cryptocarya moschata</i> Nees & Martius in Nees (1833: 37)	<i>Moraes 2355</i> (ESA)	23 Jan 2001	Brazil, São Paulo	–	HG315578
<i>Cryptocarya moschata</i>	<i>Moraes 2551</i> (HRCB)	17 Sep 2005	Brazil, São Paulo	HG314991	HG315579
<i>Cryptocarya oahuensis</i> Fosberg (1936: 3)	<i>Hawaiian Plant DNA Library 6891</i> (BISH)	27 Sep 2011	U.S.A., Hawaii	HG314992	HG315580
<i>Cryptocarya oubatchensis</i> Schlechter (1906: 110)	<i>McPherson 19131</i> (MO)	01 Nov 2003	New Caledonia	HG314993	HG315581
<i>Cryptocarya pluricostata</i> Kostermans (1974b: 43)	<i>McPherson 18471</i> (MO)	22 Apr 2002	New Caledonia	HG314994	HG315582
<i>Cryptocarya saligna</i> Mez (1889: 13)	<i>Moraes 3182</i> (HRCB)	06 Sep 2011	Brazil, Espírito Santo	HG314995	HG315583
<i>Cryptocarya saligna</i>	<i>Moraes 3226</i> (HRCB)	10 Sep 2011	Brazil, Espírito Santo	HG314996	HG315584
<i>Cryptocarya subtriplinervia</i> (Kostermans 1958: 190) van der Werff (2008: 45)	<i>van der Werff 12775</i> (MO)	27 Oct 1992	Madagascar	AJ627923	HG315585
<i>Cryptocarya triplinervis</i> Brown (1810: 402)	<i>Chase 5522</i> (K)	20 Nov 1997	Australia, Lord Howe Isl.	AJ247159	HG315586

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TABLE 1 (continued)

species	voucher	date of coll.	provenance	acc. no. trnK	acc. no. ITS
<i>Cryptocarya wiedensis</i> Moraes (2007: 121)	Moraes 2623 (HUEFS)	03 Apr 2009	Brazil, Espirito Santo	HG314997	HG315587
<i>Dahlgrenodendron natalense</i> (Ross 1973: 118) van der Merwe & van Wyk in van der Merwe <i>et al.</i> (1988: 82)	Styles 2313 (SANBI)	n/a	South Africa	HG314998	HG315588
<i>Endiandra glauca</i> Brown (1810: 402)	Clarkson 9240 (L)	28 Feb 1992	Australia	HG314999	HG315589
<i>Endiandra impressicosta</i> Allen (1942: 151)	Gray 7539 (MO)	14 May 1999	Australia	AJ627924	HG315590
<i>Endiandra lecardii</i> Guillaumin (1924: 1106)	McPherson 19147 (MO)	02 Nov 2003	New Caledonia	HG315000	HG315591
<i>Endiandra poueboensis</i> Guillaumin (1924: 1107)	McPherson 18988 (MO)	28 Oct 2003	New Caledonia	HG315001	HG315592
<i>Endiandra pubens</i> Meissner (1864: 509)	Constable 4876 (HBG)	25 May 1964	Australia	AJ247162	HG315593
<i>Eusideroxylon zwageri</i> Teijsmann & Binnendijk (1863: 280)	Arifiani 41 (MO)	08 Mar 2000	BG Bogor [Borneo, Sumatra]	–	HG315594
<i>Eusideroxylon zwageri</i>	Gwee 2004-42 (SING)	24 Nov 2004	BG Singapore [Borneo, Sumatra]	AJ627926	HG315595
<i>Hypodaphnis zenkeri</i> (Engler 1899: 385) Stapf (1909: 185)	Leeuwenberg 5557 (HBG)	24 Apr 1965	Cameroon	AJ247166	–
<i>Hypodaphnis zenkeri</i>	McPherson 16184 (MO)	12 Nov 1993	Gabon	–	HG315596
<i>Potameia chartacea</i> Kostermans (1957: 6)	van der Werff 12835 (MO)	04 Nov 1992	Madagascar	AJ627930	HG315597
<i>Potameia thouarsiana</i> (Baillon 1892: t.237) Capuron (1960: 63)	S.F. 14156 (L)	02 Aug 1955	Madagascar	HG315002	HG315598
<i>Potoxylon melagangai</i> (Symington 1940: t.3409) Kostermans (1978: 143)	Wong 325 (AAU)	05 Apr 1988	Brunei	HG315003	HG315599
<i>Ravensara elliptica</i> Kostermans (1939: 110)	Capuron 28409 (L)	Nov 1968	Madagascar	HG315004	HG315600
<i>Sinopora hongkongensis</i> (Xia, Deng & Yip 2006: 75) Li, Xia & Li (2008: 199)	Xia s.n. (MO)	2009	China	HG315005	HG315601
<i>Triadodaphne inaequitepala</i> (Kostermans 1969: 485) Kostermans (1993: 131)	Pullen 5505 (L)	30 Jul 1964	Papua New Guinea	HG315006	HG315602
<i>Yasunia quadrata</i> van der Werff & Nishida (2010: 494)	Graham 2369 (MO)	30 Jun 2003	Peru	HG315007	HG315603
<i>Yasunia sessiliflora</i> van der Werff & Nishida (2010: 494)	Pérez 4222 (MO)	28 May 2009	Ecuador	HG315008	HG315604

Sequences were aligned using the MUSCLE alignment as implemented in MEGA 5 (Tamura *et al.* 2011), using the default parameters. After automatic alignment, we made some manual adjustments guided by the following principles. 1. If an indel can be explained by a duplication of an immediately adjacent DNA motive, then this is the preferred position. 2. If indels of the same size occur in different taxa in close proximity, then it is more likely that the indel originated once than that it originated several times (unless the adjacent bases suggest the contrary, as outlined in principle 1). 3. If different equally plausible alignments would lead to different (possibly spurious) synapomorphies, and it cannot be decided which one is preferable based on overall similarity of the

sequences, then an uninformative placement of the indel is preferred. If such a placement is not possible, then the indel positions are excluded from the analysis. In general, simple indel coding following Simmons & Ochoterena (2000; see also Simmons *et al.* 2007) was applied to those informative indels that could be placed with confidence. In a few cases, however, where short insertions of different size and/or different sequence suggesting a possibly different origin have been found in the same position relative to the majority of the taxa or where indels were caused by single nucleotide repeats of different lengths, we preferred to use a single multistate character. Uninformative indels and areas of uncertain alignment (which occurred only in the ITS sequences) were excluded from the analysis. If uncertainties in the alignment involved only a few taxa, then the sequence positions of uncertain alignment were replaced by question marks in these taxa only. In the final analysis, we included only those taxa from which we were able to obtain complete, clean sequences of both the ITS region and the *trnK* intron. As a rule the two sequences were obtained from the same sample, except *Beilschmiedia tawa*, *Cryptocarya alba*, and *Hypodaphnis zenkeri*. In these species, a *trnK* intron sequence had been submitted to GenBank earlier, whereas the ITS region was sequenced here from a different collection. The final alignment is found in the supplementary data.

Phylogenetic analyses.—Data analyses employed maximum parsimony (MP) using PAUP* 4.0b10 (Swofford 2003), maximum likelihood (ML) using Treefinder (Jobb 2008), and Bayesian inference (BI) using MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003). The data from the *trnK* intron and ITS were analyzed separately as well as combined in a single analysis after the separate analyses had shown that their results were largely compatible (but not entirely, see below). If two or more sequences obtained from different collections of the same taxon turned out to be identical in all non-excluded positions, only one of them was used for the final analysis.

In the MP analysis, a heuristic search was performed with 100 random addition sequence replicates, tree bisection-reconnection (TBR) swapping, collapse of zero-length branches, and MulTrees on. All character state changes were equally weighted, and those gaps that had not been excluded were treated as missing data. Branch support was estimated by fast bootstrapping (Mort *et al.* 2000) with 100,000 replicates.

For Bayesian inference, data were divided into a total of eight unlinked partitions. Five partitions were used for the *trnK* intron data, one for the indels, one for the non-coding intron regions, and one for each of the three codon-positions of the *matK* gene. Three partitions were applied to the ITS data, one for the positions coding for ribosomal RNA (mainly the 5.8S region, plus small parts of the 18S and 26S regions), one for the non-coding ITS-1 and ITS-2 regions, and one for the indels. The most appropriate substitution models for the partitions including DNA data were estimated by MrModelTest (Nylander 2004) using MrMTgui (Nuin 2005). As suggested in the MrBayes manual, the default priors with Dirichlet proposal were used for the analysis. For each analysis, two simultaneous runs of four MCMC chains each were run for 5,000,000 generations, with the current tree saved every 500 generations. The burnin was determined by visual inspection of the likelihood values in Excel, and the posterior probabilities for the individual clades were computed by creating a majority-rule consensus of the remaining trees in PAUP.

In the ML analysis, the indel matrix could not be used, but for the DNA data the same six partitions were used as for the BI analysis. The substitution models were calculated independently for each partition using the “propose model” option as implemented in Treefinder. Branch support was estimated by partition-wise likelihood bootstrap with 1,000 replicates.

Results

Sequence characteristics.—The alignment of the 64 *trnK* sequences was straightforward. The alignment length used for the analysis was 2,606 bp, of which 125 were excluded from the analysis (all of them uninformative indels). In addition, we coded 21 potentially parsimony informative indels. Among the 2,481 included alignment positions in the *trnK* intron dataset, 2,094 were constant, 203 variable but not parsimony-informative, and 205 were potentially parsimony-informative. Including the 21 informative indels, the total number of informative characters was 226.

In the case of ITS, only the coding parts (18S, 5.8S and 26S) could be aligned without any ambiguity. In the non-coding parts (ITS-1 and ITS-2), the use of different algorithms and different parameters led to (sometimes

substantial) differences in the alignment, mainly because a few taxa (*Aspidostemon*, *Dahlgrenodendron*, *Eusideroxylon*, *Hypodaphnis*, and *Potoxylon*) differed considerably from the other included taxa and among themselves. The alignment in *Beilschmiedia*, *Cryptocarya*, *Endiandra*, *Potameia*, *Sinopora*, *Triadodaphne*, and *Yasunia*, on the other hand, was not problematic, except for few positions. Therefore, we replaced the alignment positions (nucleotides and indels) that could not be readily aligned in *Aspidostemon* (272), *Dahlgrenodendron* (154), *Eusideroxylon* (139), *Hypodaphnis* (223), and *Potoxylon* (125) by question marks (number of replaced positions in parentheses, nearly all of them in regions rich in indels). The data matrix that we finally used comprised 855 aligned positions plus 32 coded parsimony informative indels. A total of 132 positions were excluded from the analyses, most of them uninformative indels, but also a few positions of uncertain alignment. Among the 755 included alignment positions in the ITS dataset, 352 were constant, 105 variable but not parsimony-informative, and 266 were potentially parsimony-informative. In addition, 32 informative indels have been coded, so that the total number of informative characters was 298.

Phylogenetic analyses.—Statistics for the maximum parsimony analyses can be found in Table 2. The fast bootstrap trees from maximum parsimony analyses (not shown) were invariably much less resolved than the trees retrieved from the Bayesian analyses (Figs. 1–3), and only a single clade with marginal support was found to be conflicting with the result from the respective Bayesian analysis (*Endiandra glauca* and *E. impressicosta* get 53 and 54% BS as sister taxa in the maximum parsimony analyses of the ITS and the combined data sets, whereas *Triadodaphne inaequitepala* is supported as sister to *E. impressicosta* in the Bayesian analyses, with 0.95 PP in both data sets). There were, however, a few conflicts between the results from the *trnK* intron data and the ITS data. Therefore, the results of the Bayesian analyses are shown here separately (Figs. 1–3). The results of the maximum likelihood analyses were generally similar to those of the Bayesian analyses, but less resolved. There were several conflicting clades, especially in the result from the *trnK* dataset, but none of them with more than 75% BS.

TABLE 2. Statistics from the maximum parsimony analyses. The first five rows refer to the numbers of characters in the matrix

	<i>trnK</i>	ITS	combined
total characters	2627	887	3514
excluded characters	125	132	257
constant characters	2094	352	2466
uninformative characters	203	105	308
informative characters	205	298	503
no. of trees	16588	1578	9
tree length	549	1135	1700
consistency index	0.83	0.55	0.63
retention index	0.93	0.81	0.85

Among a total of 73 clades of different composition retrieved in all nine analyses, 23 are invariably present, and another 21 are compatible with all supported clades from all analyses. Among the 29 clades that were found to be conflicting with at least one other clade of at least one of the other analyses, there are only two “hard” conflicts, i.e. cases in which a well-supported clade (PP \geq 0.95 or BS \geq 90%) in one analysis conflicts with a well-supported clade in another analysis (clade 27 and clade 59 vs. clade 62). This conflict is due to a different placement of *Beilschmiedia oreophila* in the plastid *trnK* and the nuclear ITS data (described below).

The well-supported clade (clade 1) sister to the rest of the ingroup (clade 2) consists of *Eusideroxylon zwageri* and *Potoxylon melagangai*. Its sister (clade 2), comprising all other taxa, has slightly lower support. Within clade 2, *Aspidostemon parvifolium* and *Dahlgrenodendron natalense* (clade 3) are sister to the remaining taxa (clade 4). The next split in clade 4 is between the genus *Cryptocarya* (clade 5) and all other taxa (clade 6, in the following called the *Beilschmiedia* clade). Within *Cryptocarya* (clade 5), all analyses show a split between *Cryptocarya alba*, *C. oubatchensis* and *C. pluricostata* (clade 7) and all other species (clade 8). The differences among the various analyses begin above this point. Therefore, we describe in detail the result of the Bayesian analysis of the combined matrix (Fig. 1) and differences compared to the other analyses. Clades supported (mainly) by one of the

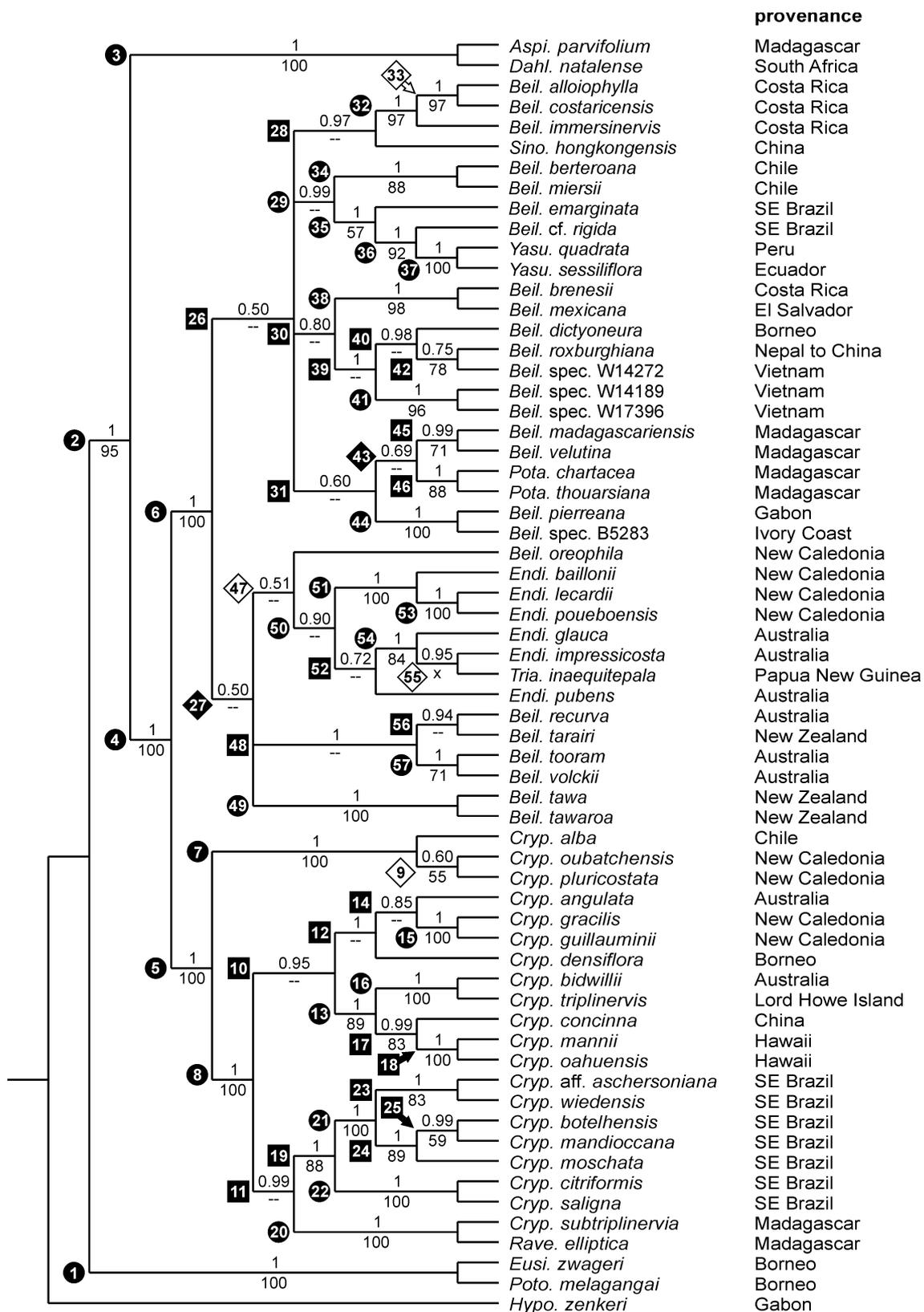


FIGURE 1. Results of the combined Bayesian *trnK* and ITS analysis. Numbers above the clades are posterior probabilities, numbers below clades are bootstrap percentages from the MP analysis based on the same matrix. Clades with <50% bootstrap support are marked with "--". An "x" indicates that there is a different clade with ≥50% support in the bootstrap consensus of the maximum parsimony analysis. Clade numbers used in the text are indicated near the base of each clade. Black circles mark clades that are present in all analyses, black squares indicate clades that are compatible with all Bayesian and maximum parsimony analyses. Diamonds mark conflicting clades; white diamonds indicate clades from the ITS data set that conflict with the result from the *trnK* intron data set, black diamonds indicate clades from the *trnK* intron data set that conflict with the result from the ITS data set.

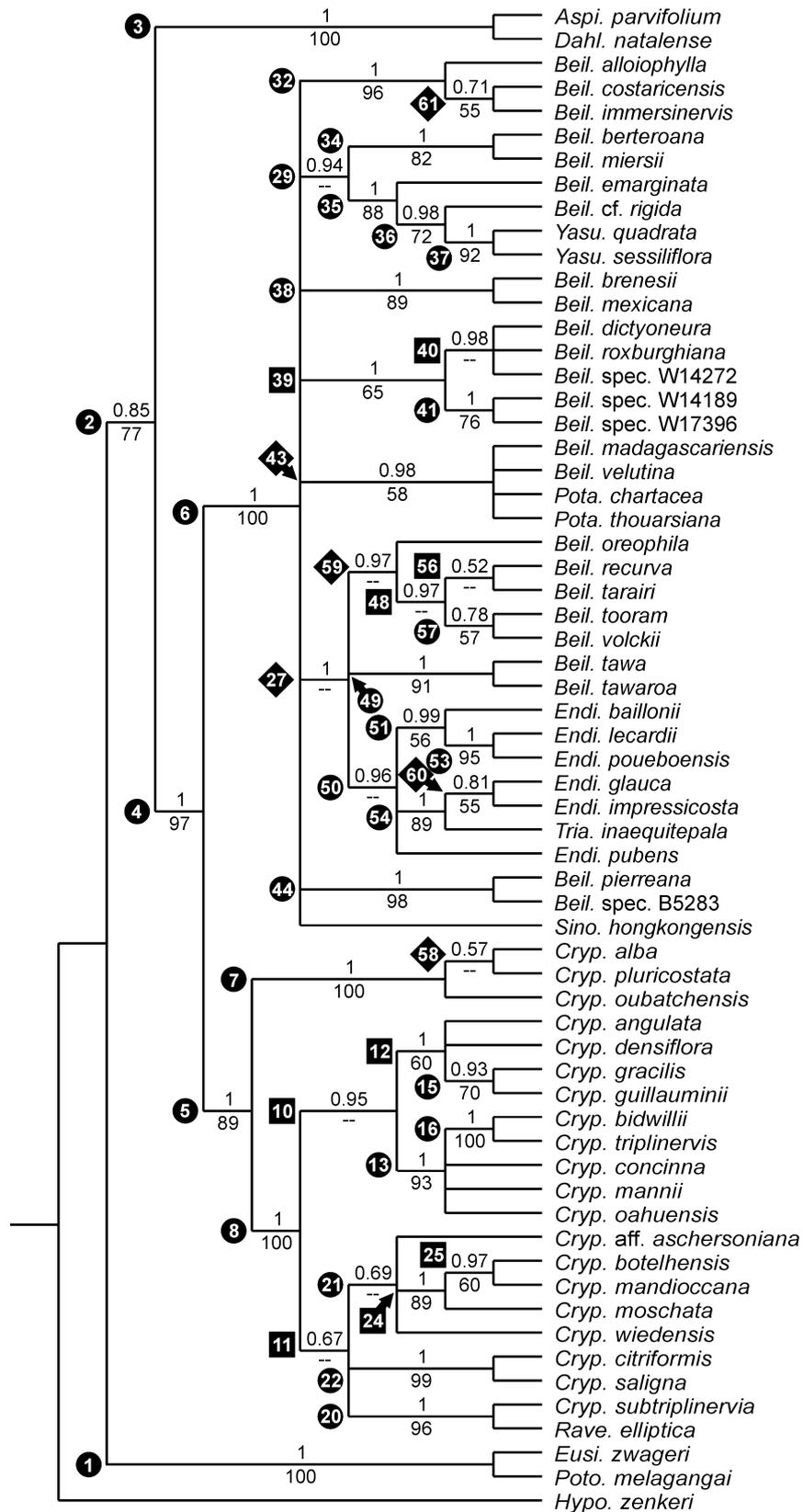


FIGURE 2. Result of the *trnK* Bayesian analysis. Numbers above the clades are posterior probabilities, numbers below clades are bootstrap percentages from the MP analysis. Clades with <50% bootstrap support are marked with "--". Clade numbers used in the text are indicated near the base of each clade. Black circles mark clades that are present in all analyses, black squares indicate clades that are compatible with all Bayesian and Maximum Parsimony analyses, black diamonds indicate clades conflicting with the result from the ITS data set.

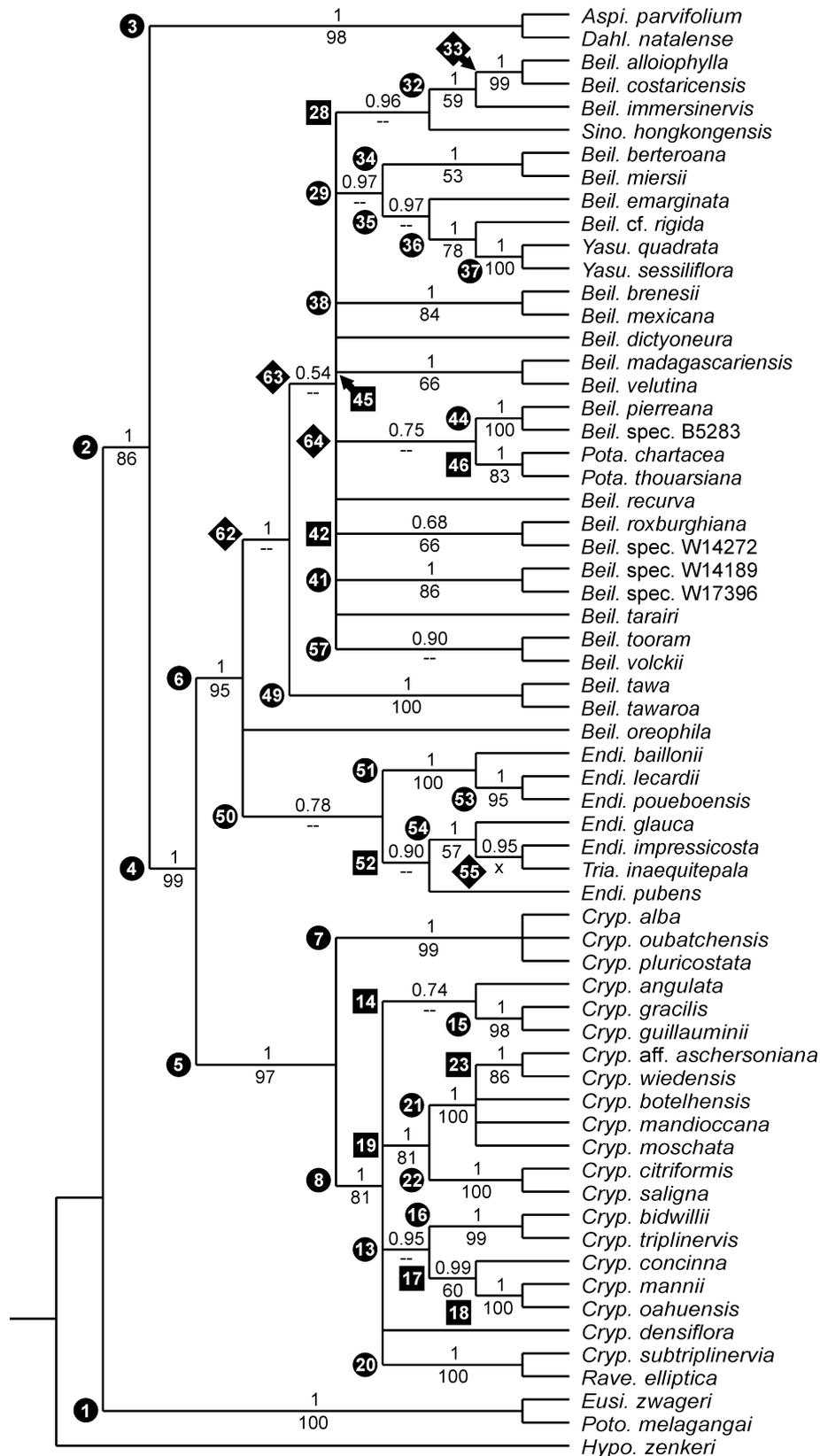


FIGURE 3. Result of the ITS Bayesian analysis. Numbers above the clades are posterior probabilities, numbers below the clades are bootstrap percentages from the MP analysis based on the same matrix. Clades with <50% bootstrap support are marked with "--". An "x" indicates that there is a different clade with $\geq 50\%$ support in the bootstrap consensus of the maximum parsimony analysis. Clade numbers used in the text are indicated near the base of each clade. Black squares indicate clades that are compatible with all Bayesian and maximum parsimony analyses, black diamonds indicate clades conflicting with the result from the *trnK* intron data set.

data sets (*trnK* or ITS) are usually compatible with the result of the other data set as well, unless otherwise stated. Within clade 7, the Bayesian analysis of the combined matrix (Fig. 1) shows *Cryptocarya alba* as sister to clade 9, which consists of *C. oubatchensis* and *C. pluricostata* and receives only low support. This topology is also retrieved by MP in the ITS data set, but it conflicts with the result from *trnK* and the ML analysis of the ITS data. Clade 8 (the rest of *Cryptocarya*) is shown as two groups, of which one (clade 10) consists of the majority of the Old World and Pacific *Cryptocarya* species (*C. angulata*, *C. bidwillii*, *C. concinna*, *C. densiflora*, *C. gracilis*, *C. guillauminii*, *C. manni*, *C. oahuensis*, *C. triplinervis*), whereas its sister group (clade 11) consists of all Brazilian *Cryptocarya* species investigated (*C. aff. aschersoniana*, *C. botelhensis*, *C. citriflora*, *C. mandioccana*, *C. moschata*, *C. saligna*, *C. wiedensis*), plus the two Malagasy species, *C. subtriplinervia* and *Ravensara elliptica*. Both clades (10 and 11) have moderate to strong support only in the Bayesian analyses. The next divergence within clade 10 is between *Cryptocarya angulata*, *C. densiflora*, *C. gracilis*, and *C. guillauminii* (clade 12), and *C. bidwillii*, *C. concinna*, *C. manni*, *C. oahuensis*, and *C. triplinervis* (clade 13). Both clades receive more support from the *trnK* data than from the ITS data. Within clade 12, the topology differs somewhat between the BI and the ML analyses. Within clade 13 *Cryptocarya bidwillii* and *C. triplinervis* form a strongly supported species pair (clade 16) sister to the remaining species (clade 17), which are supported as monophyletic by the ITS analysis only. Also the sister group relationship of the two Hawaiian species, *C. manni* and *C. oahuensis* (clade 18) gets its strong support from ITS. Within clade 11, the Brazilian species (*Cryptocarya aff. aschersoniana*, *C. botelhensis*, *C. citriflora*, *C. mandioccana*, *C. moschata*, *C. saligna*, and *C. wiedensis*, clade 19) are sister to the Malagasy species (*Cryptocarya subtriplinervia* and *Ravensara elliptica*, clade 20). The Malagasy clade is strongly supported in all analyses, whereas the Brazilian clade gets its support from ITS.

In the other major part of the ingroup, the *Beilschmiedia* group (clade 6), resolution at the base is usually poor, and/or most of the basal clades are poorly supported (e.g., clades 26 and 27, Fig. 1). There are, however, numerous less comprehensive clades that get considerable support, are invariably present, or are at least compatible with results of all analyses. Clade 28, including three Central American species (*Beilschmiedia alloiophylla*, *B. costaricensis*, and *B. immersinervis*) plus *Sinopora hongkongensis* from China, is supported only in the Bayesian ITS analyses but not by other algorithms or in analyses of *trnK* or combined data. *Sinopora hongkongensis* is shown as sister to the remaining species (clade 32), which are supported in all analyses. Clade 29 is supported by all data sets, at least with BI. It includes all South American *Beilschmiedia* species investigated and *Yasunia*, which is from South America as well. Within this clade, the two Chilean species, *B. berteriana* and *B. miersii* (clade 34), are always sister to the other four species (clade 35). Clade 35 is supported by all data sets, at least with BI. If it is present in the MP and ML analyses, then also its internal topology is the same as in the Bayesian analyses. Clade 30 is compatible with the results of all analyses and includes two Central American species, *B. brenesii* and *B. mexicana*, as well as five Asian species, viz. *B. dictyoneura*, *B. roxburghiana*, and three undetermined species collected by one of us (HvdW) in Vietnam. However, it gets weak support only in the combined BI analysis. The close relationship of the Central American species (clade 38) is supported by all data sets, but only in results from the combined data set are they sister to the Asian species (clade 39). In the combined BI analysis, the African and Malagasy *Beilschmiedia* species plus the (mainly) Malagasy genus *Potameia* form a weakly supported clade (31), which conflicts with the *trnK* ML analysis, in which the two African species are sister to the rest of the *Beilschmiedia* clade. Within clade 31, the Malagasy taxa (*B. madagascariensis*, *B. velutina* and the two *Potameia* spp. (clade 43) are sister to the African taxa, *B. pierreana* and *B. sp. (Breteler 5283)*; clade 44). The Malagasy clade (43) is only present in the *trnK* tree, which conflicts with the Bayesian ITS tree. Within clade 43, the two *Beilschmiedia* species (clade 45) are sister to the two *Potameia* species (clade 46). Both clades have support from ITS, whereas the African clade (44) is always strongly supported.

Among the remaining species (from Australia, New Zealand, New Guinea, and New Caledonia, clade 27), mainly *Beilschmiedia oreophila* is found in different positions in some analyses. Most other clades are congruent or at least compatible among the various analyses. Clade 48, consisting of *B. recurva*, *B. tooram*, and *B. volckii* from Australia plus *B. tarairi* from New Zealand, is supported by *trnK* only. The other two taxa from New Zealand, *B. tawa* and *B. tawaroa* (clade 49), are identical in both ITS and *trnK* sequences. Clade 50, including all *Endiandra* spp. as well as *Triadodaphne inaequitepala*, is supported by all data sets, at least under BI, although significantly only by *trnK*. Within clade 50, the New Caledonian *E. baillonii*, *E. lecardii*, and *E. poueboensis* (strongly supported) are sister to the remaining species (clade 52). Within it, *E. pubens* is sister to the other three species, which are retrieved (clade 54) in all analyses. The precise topology within clade 54 varies, however, among analyses.

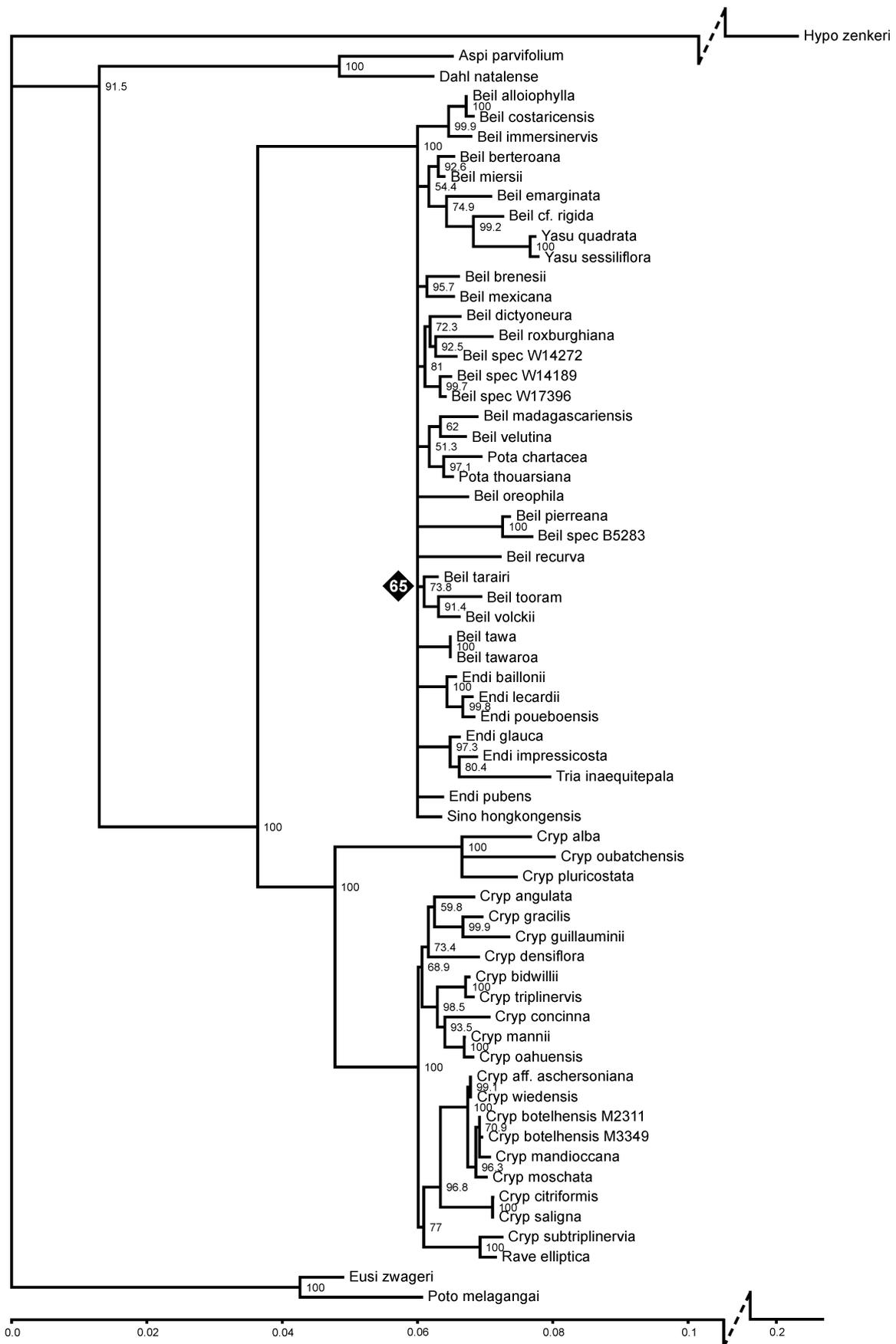


FIGURE 4. Bootstrap consensus of the maximum likelihood combined analysis. Numbers next to the nodes are likelihood bootstrap percentages, the black diamond indicating clade 65 that was retrieved in the ML analysis only.

Maximum likelihood analyses.—Results of the combined ML analysis (Fig. 4) recover almost the same topology as BI within the genus *Cryptocarya* except clade 9 is collapsed. The *Beilschmiedia* clade (6) is much less resolved, and it shows a weakly supported new clade (65) consisting of *B. tarairi* in addition to *B. tooram* and *B. volckii* (clade 57). In results of the ML *trnK* analysis (not shown) seven clades are found that have not been retrieved with other methods of analysis. All of them are weakly supported and conflict with most other results, including combined BI results. Results of the ML ITS-only analysis are still less resolved.

Discussion

Reliability of the data.—The usefulness of the plastid *trnK* intron (including *matK*) for phylogenetic inference has been shown in numerous studies on different levels from the angiosperms as a whole (Hilu *et al.* 2003 and references therein) to relationships between genera in the Lauraceae (Rohwer 2000; Rohwer & Rudolph 2005). Within genera, however, its informative value reaches its limit because there are often few or no differences between closely related taxa. The internal transcribed spacer region of the nuclear ribosomal DNA has also been widely used in many systematic studies, including Lauraceae (Chanderbali *et al.* 2001; Chanderbali 2004; Li *et al.* 2004; Rohwer *et al.* 2009). This marker is much more variable than the *trnK* intron but is difficult to align among more distantly related taxa. Combining *trnK* and ITS increases resolution as expected, but most of the lower nodes within the *Beilschmiedia* branch are still weakly supported in the Bayesian analysis and unresolved in the MP and ML analyses. Thus, conflicts between results of the *trnK* and the ITS analyses appear to be due to homoplasy, rather than to different evolutionary histories of the plastid and the nuclear genomes. Even *Beilschmiedia oreophila*, the only species involved in a well-supported conflict in our trees, shows comparable and widely overlapping p-distances to the members of the two clades with which it clusters in the different analyses (*trnK* intron: 0.00360–0.00639 to clade 48, 0.00320–0.00560 to clade 50; ITS: 0.04011–0.07056 to clade 48, 0.03748–0.05548 to clade 50).

Relationships of the genera.—The first of our questions, if *Dahlgrenodendron*, *Sinopora*, and *Yasunia* really belong to the *Cryptocarya* group, had already been answered positively at an early stage of our investigations by BLAST searches in GenBank. Therefore, we subsequently concentrated on relationships among the taxa within this group.

Monotypic *Eusideroxylon* and *Potoxylon* have always been considered closely related. Originally, *P. melagangai* was even described as a species of *Eusideroxylon*, but later Kostermans (1978) separated it because of its different androecial configuration (nine laminar stamens in *Potoxylon* vs. three columnar stamens in *Eusideroxylon*). Based on our results, *Potoxylon* should be re-united with *Eusideroxylon*. Their position as sister to the remainder of the *Cryptocarya* group had already been found by Chanderbali *et al.* (2001), albeit with weak support, in contrast to Rohwer & Rudolph (2005), who found *Aspidostemon* in this position with moderate support. In our analyses, the node linking *Aspidostemon* to all other members of the *Cryptocarya* group is moderately to strongly supported. In combination with the results of Chanderbali *et al.* (2001) that were based on a different set of molecular markers, it appears a robust assumption.

Our results clearly show that *Dahlgrenodendron* is closely related to *Aspidostemon*, not to *Cryptocarya*, in which it had been included by Kostermans (1990). *Aspidostemon* and *Dahlgrenodendron* share opposite leaves, flower buds in which the perianth is wider than long, almost sessile anthers, and mostly short inflorescences, whereas most species of *Cryptocarya* have alternate leaves, elongate flower buds, anthers with distinct filaments, and frequently also larger and more profusely branched inflorescences. However, none of these character states is without exception in the large genus *Cryptocarya*. *Aspidostemon* is, however, morphologically sufficiently homogeneous and distinct from both *Cryptocarya* and *Dahlgrenodendron* to assume that it is monophyletic. In addition, preliminary results based on partial sequences of additional *Aspidostemon* species (results not shown) consistently show them as sister to *Dahlgrenodendron*. *Dahlgrenodendron* exhibits the presumed plesiomorphic androecial configuration of Lauraceae, nine fertile stamens plus three staminodes, whereas only three or six outer stamens are fertile in *Aspidostemon* with the inner ones transformed into massive, mostly fused staminodes. In addition, *Dahlgrenodendron* differs from all other Lauraceae so far investigated in its peculiar striate pollen grains (van der Merwe *et al.* 1988).

As in the previous analyses including fewer species (Rohwer 2000; Chanderbali *et al.* 2001; Rohwer & Rudolph 2005), *Cryptocarya* is monophyletic in this analysis, and as had already been recognized earlier (van der Werff 1992) *Ravensara* needs to be included in *Cryptocarya*. New combinations and names that are necessary have been or will be published elsewhere (van der Werff 2008, 2013). *Beilschmiedia*, on the other hand, is almost certainly not monophyletic based on these results, even though the weak support of most basal nodes within the *Beilschmiedia* clade (6) leaves some uncertainty. At least *Yasunia* from South America is clearly nested among South American *Beilschmiedia* species. In addition to a few morphological characters (see below), it also shares a TATGA duplication in the *trnK* intron downstream from the *matK* gene with the *Beilschmiedia* species among which it is nested (*B. emarginata* and *B. cf. rigida*).

Also *Potameia* consistently has been found nested in *Beilschmiedia*, although associated with different species in the *trnK* and the ITS results. The best support from any analysis (0.98 PP in *trnK*) suggests that *Potameia* is most closely related to Malagasy *Beilschmiedia*. This appears to be reasonable, as the two *Potameia* species included in this study are endemic to Madagascar. The reasons why *Potameia* and *Yasunia* are not simply merged with *Beilschmiedia* have been explained in the original description of *Yasunia* (van der Werff & Nishida 2010). Obviously, the current circumscription of *Beilschmiedia*, based on morphology, is not satisfactory from a phylogenetic point of view. It appears premature, however, to make far-reaching taxonomic changes as long as it remains uncertain if and how the *Beilschmiedia* complex should be subdivided. *Endiandra* appears to be monophyletic if *Triadodaphne inaequitepala* is included, although support for this clade is really significant only in BI of *trnK*. It should be noted, however, that our analysis includes only *Endiandra* species from Australia and New Caledonia, but none from central Malesia or mainland Asia. It remains to be determined if these belong to the same clade. *Triadodaphne inaequitepala* had originally been described as an *Endiandra*, but Kostermans (1993) transferred it to *Triadodaphne*. *Triadodaphne* is supposed to differ from *Endiandra* by larger, thick and fleshy outer tepals and smaller, membraneous inner tepals as well as a deeply urceolate receptacle vs. more or less equal tepals and a much shallower receptacle in *Endiandra*. The specimen that we examined of *Triadodaphne inaequitepala*, Pullen 5505 (L), was sterile, but a paratype of the species (Pullen 5508, L), collected by the same collector from the same locality, had small but thick and fleshy inner tepals and a rather shallow receptacle (drawing available on lauraceae.myspecies.info). Therefore, we think that at least this species should be treated as *Endiandra inaequitepala* Kostermans (1969), as suggested by van der Werff (2001). Unfortunately, we were not able to get material of the type species of the genus, *T. myristicoides* Kostermans (1974a: 121), that was suitable for DNA extraction.

The question whether *Endiandra* is nested in *Beilschmiedia* or not cannot yet be answered with certainty. Based on the *trnK* analysis it appears to be nested within *Beilschmiedia* with strong support, whereas based on the ITS and combined data it may be the sister group to a weakly supported *Beilschmiedia* in the wider sense, i.e., including the other genera of the *Beilschmiedia* group. This question needs to be further investigated with additional markers and greater taxonomic sampling, particularly from the Malesian region.

The position of *Sinopora hongkongensis* also needs further study. This morphologically aberrant genus appears well supported as sister to a group of Central American *Beilschmiedia* species in the ITS and combined BI, but this topology has not been retrieved with other methods of analysis or with *trnK* alone. In all MP and ML analyses its position within the *Beilschmiedia* clade (6) is unresolved, as it is in the BI *trnK* results. We have already started a more extensive sampling of Chinese *Beilschmiedia* species with the cooperation of J. Lie (Kunming), which may help to elucidate relationships of *Sinopora*. A future study of this group should also include the genus *Syndiclis*, for which we have had no material.

Morphological considerations.—From a morphological point of view, it appears perfectly logical that *Eusideroxylon* and *Potoxylon* are sister to the rest of the *Cryptocarya* group. As in the outer androecial whorls in *Hypodaphnis*, their stamens have four separate pollen sacs in almost collateral arrangement, and their ovary is semi-inferior, only slightly less so than in *Hypodaphnis*. All other members of the *Cryptocarya* group have stamens with just two distinct pollen sacs—or at least opening by just two valves. In numerous species, there are four pollen sacs per anther, but the pollen sacs on each side appear to have fused laterally, so that they open by a single valve on each side of the anther. This is particularly obvious in several species of *Endiandra* (see Hyland 1989, Figs. 76 F and 78 B), and it has also been observed for *Cryptocarya* by Moraes (2007). We therefore assume that bilocular anthers derived by lateral fusion of the pollen sacs are a synapomorphy of the larger part of the *Cryptocarya* group. As described by Rohwer (1994), bilocular anthers in other Lauraceae appear to have arisen by reduction of either the upper or the lower pair of pollen sacs.

The characters typical of *Aspidostemon* and *Dahlgrenodendron* (opposite leaves, depressed flower buds, subsessile anthers) have already been mentioned above. *Hypodaphnis*, *Eusideroxylon*, and *Potoxylon* have alternate leaves, so that the opposite leaves of *Aspidostemon* and *Dahlgrenodendron* may be considered a synapomorphy of these genera—perhaps a reversal to the ancestral condition, as most other Laurales have opposite leaves. However, opposite leaves are also found among the remaining genera with considerable frequency, making it difficult to assess their significance. Flower bud shape and length of filaments are also variable among the other taxa, particularly within *Beilschmiedia*.

Cryptocarya is morphologically diverse, but similar enough to be characterized relatively easily, particularly in its flower structure. Flowers are invariably trimerous, with nine bilocular anthers, three relatively big cordate to sagittate staminodes, and a deep and narrow receptacular tube enclosing the ovary. In fruit, this receptacular tube becomes adnate to the ovary and complements the function of the pericarp. This type of fruit is plesiomorphic for *Cryptocarya*, as it is also found in *Hypodaphnis*, *Eusideroxylon*, *Potoxylon*, *Aspidostemon*, and *Dahlgrenodendron*. It is, however, not known from the *Beilschmiedia* clade, which is sister to *Cryptocarya*. A relatively deep, but more funnel-shaped than tubular receptacle is found in *Triadodaphne myristicoides*, but the fruit of this species is still unknown. The third species of *Triadodaphne* that has been described so far, *T. pachytepala* Kostermans (1993: 129), has a shallow receptacle, like most species of *Endiandra*.

In spite of its strong support in all analyses, the first clade within *Cryptocarya* separating from the rest of the genus (clade 8), including *C. alba*, *C. oubatchensis*, and *C. pluricostata*, does not seem to have any obvious morphological synapomorphies. The leaves of *C. alba* are opposite and usually broadly elliptic, whereas those of *C. oubatchensis* are alternate and usually oblanceolate; those of *C. pluricostata* are alternate and (ovate-)elliptic. In the last species they are densely pubescent, whereas in the other two they are glabrous or nearly so. Also in flowers and fruits, we have not found anything that would separate these three species from the rest of the genus. Among the remaining clades within *Cryptocarya*, our sampling is not yet dense enough for a definite statement on their morphological homogeneity. It is obvious, however, that the triplinerved species (*C. densiflora*, *C. subtriplinervia*, *C. triplinervis*) do not form a clade.

The *Beilschmiedia* clade (6) is characterized by flowers with a superior ovary in a relatively shallow receptacle and by fruits that are (as far as they are known) inserted free on their pedicel, not enclosed in an accrescent receptacular tube. This appears to be a synapomorphy of this clade based on the topology within the *Cryptocarya* group. In floral structures, there is far more variation in the *Beilschmiedia* clade than in its sister group, *Cryptocarya* (van der Werff & Nishida 2010, Tab.1). Dimerous flowers appear to have evolved repeatedly from normal trimerous flowers, in *Potameia* and *Yasunia quadrata* in our sample, but also in *Syndiclis* and some species of *Endiandra*. The number of fertile stamens is often reduced from the normal nine, to six, four, three, or even two. They may have four well-developed pollen sacs, (mostly) only two recognizable locules, or rarely only a single locule. The staminal glands can be normally developed, absent, or greatly enlarged to form a glandular cushion. The staminodia of the fourth androecial whorl can be large and sagittate as in *Cryptocarya* and most *Beilschmiedia* species, massive as in *Sinopora* and *Yasunia*, or small, or absent. Considering this wide range of morphological variation, resolution on the molecular level is surprisingly low. There is enough variation among the species of this group (176 parsimony-informative positions or up to 77 pairwise differences among the species), but as in the morphological characters, much of this variation seems to be due to homoplasious change. The low (well-supported) resolution among the basal nodes, in combination with our limited taxon sample and sometimes disparate descriptions of the taxa, makes it difficult to recognize morphological patterns. Therefore, we can give only some tentative suggestions so far. Besides those groups that have been treated as separate genera anyway (*Endiandra*, *Potameia*, *Yasunia*), the South American clade (29) appears to be recognizable by morphological characters, as its species (including *Yasunia*) share opposite leaves with a particularly coarse reticulation. It should be noted, however, that these characters are also found in the Central American *B. brenesii*, which is not a member of this clade in our analysis, but rather sister to *B. mexicana*, a species with alternate leaves showing the fine reticulation type described by Nishida & Christophel (1999). The remaining three Neotropical species that we investigated, *B. alloiophylla*, *B. costaricensis* and *B. immersinervis*, all have alternate leaves with fine reticulation, and they appear to be sister to the Chinese *Sinopora hongkongensis* (which also shows these characters, like most species of the *Beilschmiedia* clade). Among these, *B. alloiophylla* and *B. costaricensis* extend to northwestern South America as well (see Nishida 1999).

Among the Australian species, *Beilschmiedia tooram* and *B. volckii* share a reduction to six fertile stamens per flower. It remains to be checked if other species with a reduced number of stamens (e.g., *B. castrisinensis* Hyland [1989: 150] and *B. oligandra* Smith [1958: 28]; see Hyland 1989) are members of the same clade.

Within *Endiandra*, our taxon sampling is not yet sufficient to see if there is agreement with morphological groups described by Hyland (1989). So far, we have only a single member from three of his 10 morphological groups in our matrix, and we were not yet able to obtain reliable sequences of the species with (up to) six stamens per flower, *E. globosa* Maiden & Betche (1899: 149) and *E. montana* White (1933: 36).

Biogeographical considerations.—Although several of the basal nodes in our cladograms are either insufficiently resolved or not well supported, some geographical signal is clearly evident in our results. Almost all well-supported crown groups are geographically homogeneous or nearly so (Fig. 1). The most conspicuous exception is the relationship of the Chilean *Cryptocarya alba* to two species from New Caledonia, *C. oubatchensis* and *C. pluricostata*, which was retrieved independently in the *trnK* and ITS results, invariably with high support. We assume that this disjunction must have been caused by long distance dispersal across the Pacific. The most likely vectors for such are fruit-eating birds, even though we do not know of any regular migration routes that would link these areas. Megachiropterans, which are also fruit eaters and good flyers, are important dispersers in the Pacific region, but they apparently avoid Lauraceae (Eby 1998), presumably due to the secondary compounds contained in their fruits. The origin of *C. alba* is clearly different from that of the other South American *Cryptocarya* species, indicating two independent introductions. Several years ago, when New Caledonia was considered an ancient landmass that had persisted in isolation ever since its separation from Gondwana in the Cretaceous, this disjunction might have been considered as an example of a relictual range of Gondwana origin. However, geological studies (cited in Pillon 2012) have recently shown that New Caledonia was completely submerged until about 37 million years ago, and the levels of genetic divergence are also far too low.

Among the remaining *Cryptocarya* species (clade 8), the major well-supported clades can be characterized as Asian–Australian (clade 10), southeastern Brazilian (clade 19), and Malagasy (clade 20). The Hawaiian species *C. mannii* and *C. oahuensis*—which differ from one another by one base pair and a length difference in one of the poly-T repeats in their *trnK* sequences, and by three base pairs and a length difference in a poly-G in their ITS sequences—are clearly members of the Asian–Australian clade. Unfortunately our taxon sampling is not yet sufficient to pin down their origin more precisely. In any case, their ancestor must have reached its present range by eastward dispersal. The Malagasy clade is, according to the *trnK* analyses, apparently sister to the South American taxa (except *C. alba*). This relationship, however, appears well supported only in the combined Bayesian analysis. It remains to be seen if it is upheld when African species, additional Malagasy species, or more South American species are added to our taxon sample.

In the *Beilschmiedia* clade (6) support for the basal clades is too low to reach any definite biogeographical conclusions. During the work on our analyses, we observed that either African or Asian or Australian or Central American taxa would form the first clade that separated from the rest of the group, depending on the taxon sample, the included characters and the method of analysis but never with strong support. An Old World origin, however, has to be assumed because the basal clades of the *Cryptocarya* group are all paleotropical. In our combined results, the species from the southwestern Pacific (Australia, New Zealand, New Caledonia, New Guinea; clade 27) are sister to those from the rest of the world (clade 26), but the support for both clades is low. Within clade 26, we find a clade consisting of species from (southern) South America (clade 29), Africa and Madagascar (clade 31), and two in which a mainly Central American group is sister to an Asian group (clades 28 and 30). Also in this case it can be assumed that a migration between Asia and the Americas occurred more than once, and that the origin of the species from southern South America is probably different from that of the species from Central America (and northwestern South America). It would be tempting to think of the former as an ancient Southern Hemisphere relict and of the latter as a recent immigration after the closure of the Central American land bridge in the Pliocene, but this idea is not supported by our results, neither by the topology nor low levels of DNA divergence.

Molecular clock?—In phylogenetic studies such as this it has become common practice to estimate the divergence times of the clades based on calibration of the retrieved topology. However, the reliability of such estimates depends not only on the quality of the phylogenetic analyses, but even more on the accuracy and reliability of the calibrations (Graur & Martin 2004). In our analyses, several potentially important nodes are either poorly resolved or not well enough supported, especially in the *Beilschmiedia* clade. The calibration problem is even more serious: how can we confidently assign a fragmentary fossil to a certain clade in a group where it is

often difficult to assign the extant species to their evolutionary lineages based on morphology alone? There are some fossils that are supposed to belong to the *Cryptocarya* group, like the Miocene leaf remains described by Bannister *et al.* (2012) or those ascribed to *Cryptocarya* by Holden (1982), but it is unclear at this time how reliable these determinations are and to which taxa they should refer. Pole (1993) wrote about the material described by Holden (1982) that “[...] this cannot yet be affirmed, and placement in say, *Cinnamomum* or *Neolitsea* ruled out.” Even if it was *Cryptocarya*, this would not help in placing of the calibration point. Pole (1993) compared the fossils to “*Cryptocarya macrophylla* Guill.” from New Caledonia (probably an error instead of *C. macrocarpa* Guillaumin [1924: 1103]; at least the leaf looks like in this species) and to *C. triplinervis* from Lord Howe Island. To which clade should be given a mid-Miocene age, clade 7, 9, or 16? Instead of guessing at a possible calibration point we prefer to postpone a molecular clock analysis until we are more confident about relationships of the extant species and affinities of fossils to them.

Conclusion

The questions that we raised in the introduction can be answered as follows. (1) *Dahlgrenodendron*, *Sinopora*, and *Yasunia* are members of the *Cryptocarya* group. *Dahlgrenodendron* is sister to *Aspidostemon*, whereas *Sinopora* and *Yasunia* belong to the *Beilschmiedia* clade. *Yasunia* is nested among South American *Beilschmiedia* species. The phylogenetic position of *Sinopora* needs further study. (2) *Triadodaphne inaequitapala* is a species of *Endiandra*. It remains to be determined if this is true for the other two species of *Triadodaphne* as well. (3) *Cryptocarya* is monophyletic, in spite of its morphological diversity. *Endiandra* appears to be monophyletic as well, although a broader sampling including species from continental Asia will be necessary to confirm this. *Beilschmiedia* is clearly not monophyletic in its present circumscription. At least *Potameia* and *Yasunia* are nested among *Beilschmiedia* species, possibly also *Endiandra* and/or *Sinopora*.

In addition, our study supports the following conclusions: (a) Tetrasporangiate anthers are plesiomorphic in Lauraceae, and bilocular anthers in the *Cryptocarya* group (but not in other Lauraceae) have arisen by lateral fusion of the two pollen sacs of a theca. (b) Within the *Cryptocarya* group, a superior ovary and consequently a fruit that is free on its pedicel are synapomorphies of the *Beilschmiedia* clade. The plesiomorphic conditions appear to be an ovary that is (semi-)inferior or at least enclosed in the receptacular tube and a fruit in which the fleshy outer layers are formed by receptacular tissue. (c) The *Cryptocarya* group originated in the Paleotropics. Its two largest genera, *Beilschmiedia* and *Cryptocarya*, have reached the New World more than once, probably from different sources.

Still a number of problems remain to be investigated in further studies. The resolution among the basal lineages within the *Beilschmiedia* clade needs to be improved by additional molecular markers and collections from regions that are still relatively poorly represented in our taxon sample (e.g., tropical Africa, subtropical Asia, the Indian subcontinent, additional Malesian islands). A better circumscription or perhaps subdivision of the genus *Beilschmiedia* is needed, integrating molecular and morphological evidence. The positions of *Endiandra* and *Sinopora* relative to the remaining taxa of the *Beilschmiedia* clade need further study. The genus *Syndiclis* needs to be included, with special attention to its relationships with the morphologically similar genus *Potameia*. Also for *Cryptocarya*, additional collections are needed, e.g., from South Africa, Continental Asia and further Pacific islands. Some of these investigations are under way, but others depend on availability of suitable plant material.

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