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DAFTAR ISI

THE PHYLOGENETIC STUDY OF NEW GUINEAN SPECIES OF ENDIANDRA (LAURACEAE) AND ITS RELATIONSHIPS WITH BEILSCHMIEDIA BASED ON MORPHOLOGICAL CHARACTERS

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Deby Arifiani, Adi Basukriadi & Tatik Chikmawati 2012. Studi Filogenetik Jenis-jenis *Endiandra* (*Lauraceae*) dari New Guinea dan Kekerabatannya dengan *Beilschmiedia* Berdasarkan Karakter Morfologi. *Floribunda* 4(4): 93–102. — Spesies-spesies *Endiandra* yang berasal dari New Guinea mempunyai karakter vegetatif, bunga dan buah yang bervariasi. Karakter kelenjar benang sari dapat dijumpai pada 34 spesies dari 46 spesies yang ada di New Guinea, berbeda dengan spesies-spesies dari Borneo dan Peninsula Malaya yang bunganya tidak mempunyai kelenjar benang sari. *Beilschmiedia* merupakan genus yang sangat mirip dengan *Endiandra* secara vegetatif. Keduanya hanya dapat dibedakan dengan adanya karakter bunga. Penelitian ini bertujuan untuk mengetahui hubungan kekerabatan spesies-spesies *Endiandra* dari New Guinea dan untuk mengetahui pentingnya karakter benang sari untuk pengelompokan spesies-spesies di dalam *Endiandra*. Hubungan kekerabatan antara *Endiandra* dan *Beilschmiedia* berdasarkan karakter morfologi juga akan dibahas. Analisis filogenetik telah dilakukan menggunakan 47 karakter morfologi dari 50 taksa, yang terdiri dari 41 spesies *Endiandra* dan 6 spesies *Beilschmiedia* (sebagai in-groups) dengan 3 spesies *Cryptocarya* (sebagai outgroups). Pohon filogenetik dikonstruksi menggunakan metode Maximum Parsimony dan menunjukkan bahwa 47 taksa in-goups mengelompok dalam 5 klad tetapi hanya didukung oleh nilai bootstrap yang rendah. Spesies-spesies *Endiandra* antara yang mempunyai dan tidak mempunyai kelenjar benang sari saling mengumpul menjadi satu. Oleh karena itu, status *Endiandra* dan *Beilschmiedia* serta pentingnya karakter kelenjar benang sari belum dapat dipastikan, karena dukungan *Bootstrap* yang rendah.

Kata Kunci: *Beilschmiedia*, klad, *Endiandra*, kelenjar benang sari, New Guinea.

Deby Arifiani, Adi Basukriadi & Tatik Chikmawati 2012.The Phylogenetic Study of New Guinean Species of *Endiandra* (*Lauraceae*) and Its Relationships with Beilschmiedia Based on Morphological Characters. *Floribunda* 4(4): 93–102. — *Endiandra* species from New Guinea consist of species which vary in vegetative and reproductive characters. Staminal glands are present in 34 species out of 46 species of *Endiandra* in New Guinea, in constrast to the Bornean and Malay Peninsular species that lack of staminal glands. *Beilschmiedia* is a genus that often confused with *Endiandra* vegetatively, only flower characters can differentiate the two genera. This study was aimed to understand relationships of *Endiandra* species in New Guinea and to know the importance of staminal glands in grouping the New Guinean species of *Endiandra*. The relationships between *Endiandra* and *Beilschmiedia* based on the morphological characters will also be discussed. A phylogenetic analysis was performed to 47 morphological characters from 50 taxa, consisted of 41 species of *Endiandra* and 6 species of *Beilschmiedia* (as in-groups) with 3 species of *Cryptocarya* (as outgroups). Phylogenetic tree was constructed using Maximum Parsimony method. Phylogenetic tree showed that 47 in-groups taxa were grouped into five clades however with low bootstrap support. The species with and without glands are not separated from each other. Therefore, because of low bootstrap support, the monophyly of *Endiandra* and *Beilschmiedia* and the importance of staminal glands cannot be confirmed.

Keywords: *Beilschmiedia*, clade, *Endiandra*, staminal gland, New Guinea.

Endiandra R.Br. is a member of *Lauraceae*, a family of about 50 genera with 2500–3500 species (Rohwer 1993). The generic delimitation in the family are mainly based on the floral morphology (Nees 1836, Meissner 1864, Mez 1889, Kostermans 1957). *Endiandra* is a genus consists of over 100 species which was first described by Robert Brown in 1810 for a single species from

New South Wales (Australia), *Endiandra glauca*. The species can be characterized by paniculate inflorescence in which the ultimate cyme is not strictly oppposite, bisexual flowers, stamens 3 (rarely 2 or more than 3) with 2 locules of anthers and fruits are free on receptacles. *Endiandra* is grouped together with the genera *Beilschmiedia*, *Potameia*, *Cryptocarya* and *Triadodaphne*e in the tribe *Cryptocaryeae* based on the paniculate inflorescence (Werff & Richter 1996). *Endiandra* is very close to *Beilschmiedia* vegetatively, and both can only be separated by observing flowering specimens. Typical flowers of *Endiandra* has 3 stamens, whereas *Beilschmiedia* has 9 stamens (Figure 1). Therefore, it is rather difficult to determine the correct genus without a flowering specimen (Werff 2001). Based on sterile specimens, misidentification frequently occurred and lead to critical problems for further research. Misidentification will lead to wrong interpretation of the respective research results. A correct species name is required for further research such as research on species bioprospectings for medicines and study on species relationships.

Beilschmiedia is first described by Nees (1831) with type species of *B. roxburghiana* Nees. It has paniculate inflorescence, flowers trimerous, bisexual, stamen 9 or 6, with or without glands, anther 2-locules, and fruits are free on pedicel. The genus consists of about 250 species and has pantropical distribution (Rohwer 1993, Nishida 2001).

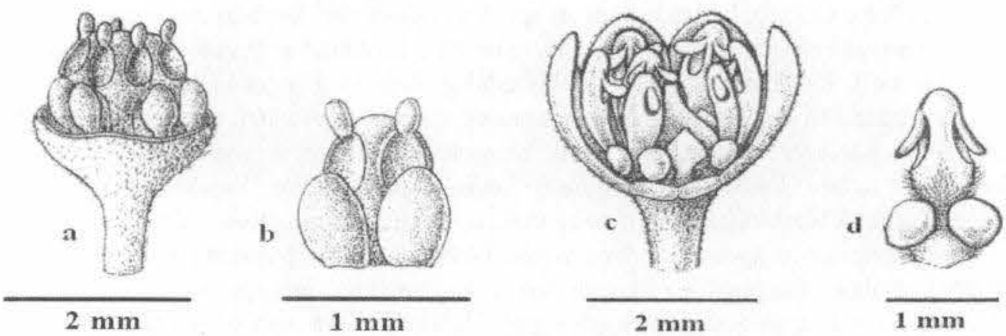

Figure 1. Flowers of *Endiandra* and *Beilschmiedia*, a. flower with 3 stamens, b. a stamen with a pair of glands (*E. grandifolia* from *Hoogland 4919*); c. flower with 9 stamens, 2 stamens were removed, b. a stamen with a pair of glands (*B. recurva* taken from Hyland 1989).

Morphologically, variation of vegetative and floral characters within *Endiandra* has created the diversity of the species. Floral characters vary with flower component differences forming the flowers. Basic floral parts are tepals, stamens and a pistil. Some species accommodate extra floral parts such as extra-staminal glands and staminodia. The type species *E. glauca* has fused glands forming skirt-like appendages surrounding stamens. Later, Blume erected a new genus, *Dictyodaphne*, with the type species from Indonesia, *D. rubescens*, with the absence of glands in its flowers (Blume 1850). Blume then realized the similarity between *Endiandra* and *Dictyodaphne* and indicated that *Dictyodaphne* may be a subgenus of *Endiandra*. However, the subdivision within *Endiandra* was not established, instead, *Dictyodaphne* has become synonym of *Endiandra*. Interestingly, through time, with more species have been described, variation of flowers in *Endiandra* still exists. Most of Australian species have flowers that bear glands (Hyland 1989) and Bornean species have showed the absence of glands in the flowers (Arifiani 2001). These facts have elevated the existence of a group of species that have *Dictyodaphne* characteristics.

Based on the specimens observation and references on *Endiandra* (Kochummen 1989, Hyland 1989, Arifiani 2001), the presence and absence of glands in the flowers of *Endiandra* seem to support the grouping within *Endiandra* by dividing the genus into two groups, i.e.: 1) a group that consists of species that have extra flower parts such as glands and 2) a group with species that bear basic flower parts with no glands or other parts. First group will represent *Endiandra* group as Brown first described the genus and second group will represent species that have *Dictyodaphne* characteristics. Therefore, it is interesting to know if staminal glands can be used for grouping within *Endiandra*. Up to now, a phylogenetic analysis has never been performed to understand the relationships within *Endiandra* based on morphological characters, with emphasis to understand the importance of staminal glands for grouping. Therefore, the phylogenetic analysis using morphological characters was carried out with aims were 1) to understand the relationships of *Endiandra* species in New Guinea; 2) to know the distribution of glandless species and species with glands in the cladogram and 3) to analyze the phylogenetic relationships of two closely related genera *Endiandra* and *Beilschmiedia* based on the morphological characters.

MATERIALS AND METHODS

Materials

The characters were observed and noted based on the herbarium specimens available at the Herbarium Bogoriense (BO) and loan specimens from the Singapore Botanic Gardens (SING). Characters of 50 taxa were included in the analysis, consisting of 41 species of *Endiandra* from New Guinea, 6 species of *Beilschmiedia* and 3 species of *Cryptocarya* (Table 1). *Cryptocarya* species were selected for outgroups as they were more distantly related to *Endiandra* than *Beilschmiedia* within the tribe *Cryptocaryeae* (Werff & Richter 1996). Additionally, *Cryptocarya* is the closest relative for both *Endiandra* and *Beilschmiedia* (Rohwer 2000, Chanderbali et al. 2001).

Methods

Characters used for phylogenetic analysis

A total of 47 characters was chosen for this analysis (Table 2 & 3) and will be discussed briefly below. The characters were observed based on the herbarium specimens of *Endiandra* from New Guinea at the Herbarium Bogoriense and scored for the cladistic analysis. The characters of *Beilschmiedia* and *Cryptocarya* were obtained from species descriptions in the publication (Hyland 1989). Twig characters used in this analysis were the color of dried twig surfaces, the presence of lenti cell and indument, indument types and orientation (Character 1–6). The color on dried twig varies from whitish to dark brown, most twigs were brown when dried and whitish twigs are limited to some species only. Three indument types were observed in *Endiandra*, i.e., straight, wavy and curly with different orientation. The straight indument can be appressed to the surface or erect, however wavy and curly induments were usually erect. Some species of *Endiandra* provide insect (ants) a place for laying eggs (called domatia) and the hollow twigs created by ants when they penetrated the twig to hide the eggs.

Leaf characters observed were leaf bud, leaf arrangement, leaf venation, petiole and leaf texture. Indument on leaf surface was also included as in twig characters (Character 7–15). Midrib, lateral vein, and minor venation were quite variable in *Endiandra* (Character 16–22), leaf domatia (Character 23) as a result of eggs laid by insect was present in *E. chyphellophora* and *E. schlechteri*. Inflorescence characters (Character 24–26) were scored for inflorescence bract, indument, and flower number. Inflorescence bracts were present in *E. gemopsis* and *E. grandifolia*. Floral characters (Character 27–31) included were floral bract and opening, pedicel and indument on tepal surface. Floral parts including staminal glands, stamens, anthers, staminodes, and ovary were included in character 32–44. Staminal glands, stamens and staminodes were scored based on their position in the staminal whorls. Fruit characters (45–47) used were position of ovary, presence of perianth remnant and presence of floral tube. Some characters were unknown, in such case missing characters were coded as (?). Each character of each taxon used for the cladistic analysis was scored as shown in Table 2 and then a data matrix was created to perform the analysis. The data matrix is shown in Table 3.

Phylogenetic Analysis

Fifty taxa and 47 characters were used in the phylogenetic analysis. In-groups consisted of 41 species of *Endiandra* and 6 species of *Beilschmiedia*. *Beilschmiedia* was included in the analysis to clarify its relationships with *Endiandra*. Three species of *Cryptocarya* as the closest relative of *Endiandra* and *Beilschmiedia* were used as outgroups (Rohwer 1993, Werff & Richter 1996, Werff 2001). Phylogenetic interpretations of the morphological characters were undertaken using PAUP program (Swofford 1998) to perform a maximum parsimony analysis, searching for shortest trees. A heuristic search for most-parsimonious trees was performed with stepwise simple addition and Tree-Bisection-Reconnection (TBR) branch swapping. Characters were treated as unordered and having equal weight. Consistency index (CI) and retention index (RI) were calculated to know the quality of the tree. Consistency index (CI) measured the amount of homoplasy in a character data set in relation to cladogram and RI was calculated to measure the amount of similarity in a character that can be interpreted as synapomorphy on a cladogram (Kitching et al. 1998). Bootstrap analysis was performed to test the tree topology stability (Felsenstein 1985).

Table 1. Taxa included in the phylogenetic analysis

No	Species	Distribution	Voucher
1	*E. aggregata*	PNG	Clemens 1421 (BO)
2	*E. archiboldiana*	PNG	Brass 3813 (BO)
3	*E. areolata*	W Papua	Pleyte 733; Brass & Versteegh 13142 (BO)
4	*E. arfakensis*	W Papua	Mayr 184 (BO)
5	*E. asymmetrica*	Moluccas, W Papua, PNG	Brass 6921, 14101, 32429; Clemens 1742, 1848 (BO)
6	*E. aurea*	W Papua	Kostermans 2014 (P); following Kostermans (1950)
7	*E. beccariana*	Moluccas, W Papua	Kostermans & Tangkilisan 146 (BO)
8	*E. carrii*	PNG	Carr 13849 (BO)
9	*E. crassipetala*	PNG	Henty NGF29370 (BO)
10	*E. cupulata*	W Papua	Koster BW1344 (BO)
11	*E. cyphellophora*	PNG	Carr 15379, 15380 (L); following Kostermans (1950)
12	*E. dielsiana*	PNG, Queensland	Hyland 13176; Kostermans 2004 (BO)
13	*E. djamuensis*	PNG	Schlecter 17341 (BO)
14	*E. euadenia*	PNG	White NGF10252 (BO)
15	*E. faceta*	PNG	Carr 12195 (BM, L); following Kostermans (1969)
16	*E. flavinervis*	PNG	Gillison NGF25065; Henty NGF27344; Womersley NGF5281, NGF15379 (BO)
17	*E. forbesii*	Moluccas, PNG	Kostermans & Tangkilisan 136; Rastini 190 (BO)
18	*E. fulva*	W Papua, PNG	Royen NGF5124 (BO)
19	*E. gem*	W Papua	Anta 64 (BO)
20	*E. gemopsis*	W Papua	Royen & Sleumer 6877 (BO)
21	*E. glauca*	PNG, Queensland	Brass 8589; Gray 3211; Hyland 11598 (BO)
22	*E. grandifolia*	W Papua, PNG	Clemens 2110; Hoogland 4919; Kairo 426; Katik W2776 (BO)
23	*E. hypotephra*	W Papua, PNG, Queensland	Grey & White NGF 10377; Hyland 12476; Kanehira & Hatusima 13097; Mueller s.n. (BO)
24	*E. impressicosta*	W Papua, PNG, Queensland	Brass 7619; Balgooy & Mamesah 6228 (BO)
25	*E. inaequitepala*	PNG	Carr 16082; Pullen 5556 (BO)
26	*E. invasorium*	PNG	Eddowes & Kumul NGF13129 (BO)
27	*E. kassamensis*	PNG	Coode & Dockrill 32655; Womersley & Vandenberg 37195 (BO)
28	*E. lanata*	PNG	Croft LAE68764 (BO)
29	*E. latifolia*	W Papua, PNG	Hoogland 4585; Iwanggin BW9047; Pullen 5568 (BO)
30	*E. ledermannii*	PNG	Ledermann 6679 (BO)
31	*E. macrostemon*	PNG	Havel NGF17375 (BO)
32	*E. minutiflora*	PNG	Floyd, Gray & Middleton NGF8065, 8073 (BO)
33	*E. Montana*	PNG, Queensland	Brass 7465; Hyland 9343 (BO)
34	*E. multiflora*	W Papua, PNG	Koster BW6976 (BO)
35	*E. papuana*	Celebes, W Papua, PNG	Branderhorst 263; Clemens 1782 (BO)
36	*E. pilosa*	PNG	Kairo NGF44085 (BO)
37	*E. rifaiana*	Aru island, W Papua, PNG	Buwalda 5396, 401; Reksodihardjo 238 (BO)
38	*E. schlecteri*	PNG	Hoogland 8947 (BO); following Teschner (1923)
39	*E. sericea*	PNG	Hartley 10510; Henty NGF14808; Royen NGF20161(BO)
40	*E. sleumeri*	W Papua, PNG	Pullen 5782; Royen & Sleumer NGF7732 (BO)
41	*E. xylophylla*	PNG	Carr 14610; Streimann NGF26182 (BO)
42	*B. castrisinensis*	Queensland	Following Hyland (1989)
43	*B. obtusifolia*	Sumatra, Borneo, Java, Celebes, New Guinea	Following Hyland (1989)
44	*B. recurva*	New Guinea and Queensland	Following Hyland (1989)
45	*B. dictyoneura*	Sumatra, Borneo, Java, Celebes, New Guinea	Following Nishida (2008)
46	*B. gemmiflora*	Sumatra, Borneo, Java, Celebes, New Guinea	Following Nishida (2008)
47	*B. kuntsleri*	Malay Peninsula, Sumatra, Borneo, Thailand	Following Nishida (2008)
48	*C. brassii*	New Guinea, Cape York Peninsula (Australia)	Following Hyland (1989)
49	*C. densiflora*	Java to New Guinea, up to Queensland	Following Hyland (1989)
50	*C. mackinnoniana*	The Philippines, New Guinea, Queensland	Following Hyland (1989)

Table 2. Characters and character states used in the phylogenetic analysis

No	Characters	Character states (scored)
1	Bark color	dark-brown (0), whitish (1)
2	Twigs surface	without lenticell (0), with lenticell (1)
3	Hair on twig surface	glabrous (0), pubescent (1), densely pubescent (2)
4	Hair type on twig surface	glabrous (0), straight (1), wavy (2), curly (3)
5	Hair orientation on twig surface	glabrous (0), appressed (1), erect (2)
6	Twigs	solid (0), hollow (1)
7	Leaf buds	sparsely pubescent (0), densely pubescent (1)
8	Leaf arrangement	alternate (0), subopposite (1), slightly clustered (2)
9	Leaf venation	pinnately-veined (0), tripli-veined (1)
10	Petiole	slender (0), thick (1)
11	Petiole upper surface	flat (0), canal (1)
12	Hair on petiole	glabrous (0), pubescent (1), densely pubescent (2)
13	Leaf texture	chartaceous(0), subcoriaceous (1), coriaceous (2), stiffly coriaceous (3)
14	Lower leaf surface	glabrous (0), pubescent (1), densely pubescent (2)
15	Lower leaf surface	not glaucous (0), glaucous (1)
16	Midrib on upper surface	flat (0), impressed (1), slightly raised (2)
17	Lateral veins orientation	diverging (0), spreading (1)
18	Lateral veins	clear (0), obscure (1)
19	Lateral veins	flat (0), impressed (1), slightly raised (2), obscure (3)
20	Minor venation reticulation	coarse (0), fine (1), obscure (2)
21	Minor venation on upper surface	raised (0), obscure (1)
22	Minor venation on lower surface	raised (0), obscure (1)
23	Leaf domatia	absent (0), present (1)
24	Hair on inflorescence	glabrous (0), pubescent (1), densely pubescent (2)
25	Inflorescence bract	absent (0), present (1)
26	Number of flower in inflorescence	many-flowered (0), few-flowered (1)
27	Floral bract	absent (0), present (1)
28	Pedicel	thin (0), thick (1)
29	Flower opening	erect (0), half-erect (1), spreading (2)
30	Tepal outer surface	glabrous (0), pubescent (1), densely pubescent (2)
31	Staminal glands	absent (0), present (1)
32	Staminal glands separate	absent (0), present (1)
33	Staminal glands adnate to filament	absent (0), present (1)
34	Staminal glands fused (ring-like)	absent (0), present (1)
35	Stamens number	9 (0), 6 (1), 3 (2)
36	Stamens in the 1st whorl	absent (0), present (1)
37	Stamens in the 2nd whorl	absent (0), present (1)
38	Stamens in the 3rd whorl	absent (0), present (1)
39	Anther	glabrous (0), pubescent (1)
40	Anther locule	roundish (0) slit-like (1)
41	Staminodes	absent (0), 3 (1), 6 (2)
42	Staminodes in 3rd whorl	absent (0), present (1)
43	Staminodes in 4th whorl	absent (0), present (1)
44	Ovary	glabrous (0), pubescent (1)
45	Ovary	inferior (0), superior (1)
46	Fruit tip	with perianth remnant (0), without perianth remnant (1)
47	Fruit	entirely enclosed in enlarged floral tube (0), free on the pedicel (1)

Table 3. Data matrix used in the phylogenetic analysis by using Maximum Parsimony method

Taxon/Character number	11111111122222222223333333333444444444 12345678901234567890123456789012345678901234567
E. aggregata	00000110011010000000000010010021100200110101011 1
E. archiboldiana	00000011010010000011000101000111002001001010111
E. areolata	00000012001030001120000100000011002001000000111
E. arfakensis	0011100000110000000000010100?110012001?10000111
E. asymmetrica	00000010001020001001000100001111002001101010111
E. aurea	0121001101012200013211020?110211002001000000111
E. beccariana	00212010000111001011000101002010012001000000111
E. carrii	00000010000021000010100201001111002001101010111
E. crassipetala	00000010000021000010100201001111002001101010111
E. cupulata	00000012001010001000000200102111002001101010111
E. cyphellophora	000000110010200000000011000001000020 01?00000111
E. dielsiana	00111011000021100000000000000201100200110101011 1
E. djamuensis	0011100000001002003110010100?000002001100000111
E. euadenia	10000010011020010011110200012210012001000000111
E. faceta	10000010000020020000100101002000002001100000111
E. flavinervis	01000010001011101001000200002210012001000000111
E. forbesii	00111010011011110011000201002210012001000000111
E. fulva	00000010000020001001000100001111002001001010111
E. gem	0011101000100001001100010?00?111002001?0000?111
E. gemopsis	11111010011000010001000211110210012001000000111
E. glauca	00211010001201111011000201102110012001000000111
E. grandifolia	01232010011222001011100210102211002001101010111
E. hypotephra	00000010001200111011000201102110012001000000111
E. impressicosta	00000010001020011132110100002000002001110000111
E. inaequitepala	0100001001110000102000010000220000 2001?00001111
E. invasorium	00232010000111000001110200102210102001001010111
E. kassamensis	00000010001020000020000100000100002001001010111
E. lanata	00232010000101110001000200102210012001000000111
E. latifolia	00232010010222001001100200100111002001000000111
E. ledermannii	00000010001020001120000101001111002001001010111
E. macrostemon	000000?1001001001020000201002200002001100000111
E. minutiflora	00000110001000000010100100101111002001001010111
E. montana	0000001100101000103000010000201100101 11?0000111
E. multiflora	00000010001121001120000200000211002001001010111
E. papuana	00212010010211101001100200002210012001000000111
E. pilosa	002220100 1?202020010000200101111002001001010111
E. rifaiana	00111012001111101001000200002211002001001010111
E. schlecteri	00000000001000000000001101100111002001001010111
E. sericea	00111010011112001001000200101211002001001010111
E. sleumeri	01111010010121020011110200001211002001001010111
E. xylophylla	00132011010121000011100201001211002001001010111
B. castrisinensis	00111010000011121000000110000100001110002110111
B. dictyoneura	00111000001010110020010100000000001110002110111
B. gemmiflora	0013201200100001002110011000111100011 10?1010111
B. kuntsleri	0113201001002001001000010000111100011 10?1010111
B. obtusifolia	0011101000101102102000011000011100011 11?1010111
B. recurva	00111010001011121020000110000111000111101010111
C. mackinnoniana	0021201001112111100100010001011100011 10?1010000
C. brassii	00212010001101110000000110000111000111001010000
C. densiflora	0011101010101111110100001000102110001110?1010000

Note: missing characters were coded as "?".

RESULTS

The parsimony analysis produced 86 equally most parsimonious trees, one of the parsimonious trees is shown in Figure 2. Their length was 296, CI = 0.220, RI = 0.588. Of 47 characters used, 3 characters were parsimony-uninformative and 44 characters were parsimony-informative. Overall, phylogenetic tree showed low bootstrap support, only two clades of *Endiandra* have bootstrap values higher than 50 %. Two clades consisted of *E. Djamuensis* - *E. faceta* and *E. glauca* - *E. hypotephra* were supported with bootstrap values of 59% and 66% respectively.

The phylogenetic analysis was performed to show the relationships of *Endiandra* species occurred in New Guinea and the relationships between *Endiandra* and its closely related genus, *Beilschmiedia*. One of the parsimonious tree showed that *Endiandra* species were grouped into six clades (clades I–VI), and separated from all *Beilschmiedia* species (clade VII). The species of *Endiandra* that have staminal glands were grouped together with the species that do not have staminal glands.

Clade I of the phylogenetic tree consisted of *E. arfakensis*, *E. gem*, *E. glauca*, *E. hypotephra*, *E. euadenia*, *E. gemopsis* and *E. forbesii* and clade II consisted of *E. invasorium*, *E. lanata*, *E. papuana*, *E. beccariana* and *E. flavinervis*. The characters that unite clades I and II are solid twig; alternate and pinnate leaves; clear lateral vein; absence of domatia; presence of separate, adnate or fused staminal glands; and 3 stamens in the 3rd whorl. Clade III consists of *E. aurea*, *E. latifolia*, *E. grandifolia*, *E. pilosa*, *E. xylophylla*, *E. sleumeri*, *E. sericea* and *E. rifaiana*. They are grouped together in clade III by characters such as dark brown and solid twig; dense pubescent leaf bud; pinnate leaves; absence of domatia; presence of staminal glands, all are separate; and stamens 3, in the 3rd whorl.

Endiandra dielsiana was placed as a single lineage in the cladogram. There is no unique character observed in *E. dielsiana* to explain such position. Addition of more characters and more taxa may change the placement of *E. dielsiana*. Clade V consisted of *E. djamuensis*, *E. faceta*, *E. cyphellophora*, *E. impressicosta*, *E. montana*, *E. inaequitepala*, *E. macrostemon*, *E. crassitepala*, *E. kassamensis*, *E. areolata*, *E. multiflora*, *E. ledermannii*, *E. asymmetrica* and *E. fulva*. Some characters shared by the clade are solid twig; pinnate, shiny (not glaucous) leaves; absence of inflorescence and flower bracts; thin pedicel; staminal glands could be absent or present, all separate when present; stamens 3 or 6, in the 3rd whorl or in the 2nd and 3rd whorls, respectively. The clade consisted of both species without and with staminal glands. The upper part from *E. djamuensis* to *E. kassamensis*, consisted of species without staminal glands except for *E. montana*, that has small separate glands with 6 stamens at the 2nd and 3rd whorls. In contrast, lower part of clade V from *E. areolata* to *E. fulva*, consisted of species with staminal glands. *Endiandra montana* was not grouped together in the lower part of clade V probably because of the absence of staminodes that is shared by most of upper clade V members. Other characters shared by *E. montana* with members of upper clade V are subopposite and subcoriaceous leaves; spreading flowers; and roundish anther locules. Clade VI consists of *E. minutiflora*, *E. schlechteri*, *E. aggregata*, *E. cupulata*, *E. archiboldiana* and *E. carrii*. The shared characters are twig dark brown, without lenticell, glabrous; pinnate leaves; petiole glabrous; lower leaf surface shiny (not glaucous); midrib flat above; lateral veins raised above; staminal glands separate; stamens 3 reside in the 3rd whorl; anther locule roundish; and staminodes 3, in the 4th whorl.

The phylogenetic tree resulted from the Maximum Parsimony analysis has shown that *Endiandra* and *Beilschmiedia* were separated, indicating that both genera are monophyletic. *Beilschmiedia* was placed in clade VII, separated from all *Endiandra*. Clade VII consists of 6 species of *Beilschmiedia* that shared dark brown, pubescent and solid twig; leaves pinnate; petiole glabrous; domatia absent; inflorescen pubescent; flowers many; floral bract absent; pedicel thin; and ovary glabrous. *Beilschmiedia castrisinensis* and *B. dictyoneura* are grouped together because both have 6 stamens and 6 staminodes, whereas the rest of *Beilschmiedia* in the clade have 9 stamens with 3 staminodes.

DISCUSSION

The relationships of *Endiandra* species in New Guinea shown in the phylogenetic tree (Figure 2) have indicated that *Endiandra* is a monophyletic group. The species of *Endiandra* from New Guinea were grouped in six clades but the relationships are only supported by low bootstrap support. Low bootstrap support was probably due to limited number of characters used in the analysis (Li & Christophel 2000). The number of stamens thought earlier to be an important character to recognize genera turned out to be the opposite. *En-*

diandra montana, a species with six stamens was in the same group with species of *Endiandra* that have three stamens.

The presence and absence of staminal glands in *Endiandra* species are not grouped well in the phylogenetic tree (Figure 2). The species without staminal glands were grouped together with the species with staminal glands in clade V, even though species with glands are grouped together in clade I, II, III, IV and VI, but only with low bootstrap support. The species with fused glands are almost nicely grouped together in clade I, but 1 species in the clade has separate glands (*E. gem*). Therefore, grouping based on the gland arrangement is also not well supported. The flowering specimen of *E. gem* however was not available, the information on the gland arrangement was obtained from the perianth remnant at the base of the

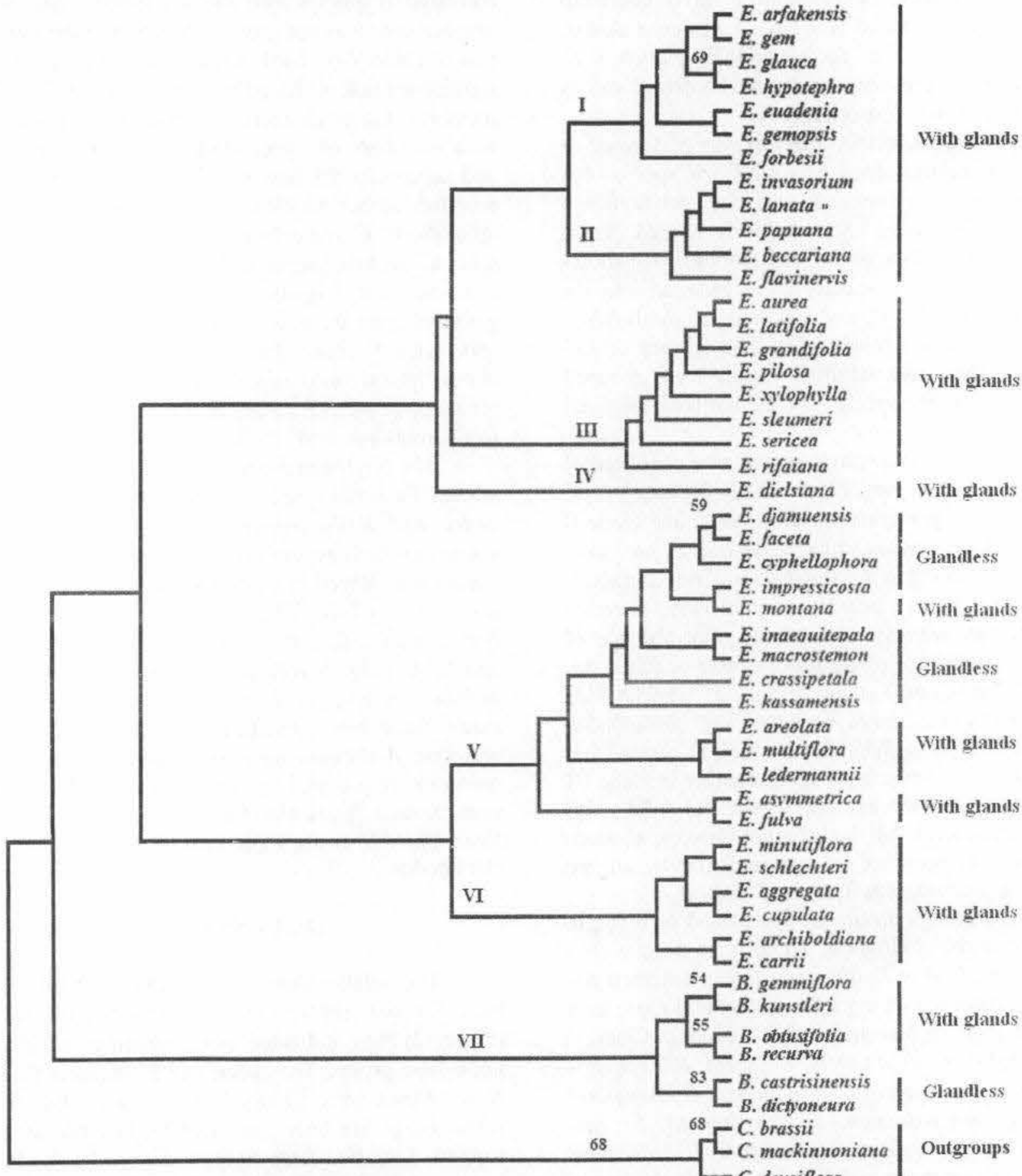

Figure 2. One of the 86 most parsimonious trees obtained from parsimony analysis of morphological character using PAUP (length = 296; CI = 0.220; RI = 0.588). Internal support was indicated by bootstrap values that are shown above the branches.

fruits (Kostermans 1969). It is interesting to know the floral characters when the flowering specimens are become available. In this study, *Endiandra* species with glands are greater in number than glandless species. This probably was caused by the union of New Guinea and Australia geologically in the past so that the New Guinean *Endiandra* species are similar to Australian species in which species with glands are dominant. Moreover, in accordance with high plant diversity in New Guinea (Welzen et al. 2005), the insect diversity is also probably high so that *Endiandra* flowers compete to attract the insects, and flowers with glands are successful because they provide nectar to the insects. According to Armstrong & Irvine (1990) and Rohwer (2009), the glands secrete nectar consisted of sugar that will attract insects to come by the flowers. Attracted insects enable pollination to occur and therefore it guarantees the fruit and seed sets. In other words, the glands are important for plant survival because the glands gives an advantage of increasing fruit set which increases the chances of fruits are being dispersed by birds. Consequently, more species may grow in other places.

The present analysis indicated that *Endiandra* and *Beilschmiedia* are monophyletic groups with characters separating *Endiandra* and *Beilschmiedia* are the stamens and staminodes. Their number and position in the floral whorl separate the two genera. *Endiandra* has 3 or 6 stamens in the 3rd whorl or 2nd and 3rd whorls (respectively), versus 9 or 6 stamens in the 1st, 2nd and 3rd whorls or 1st and 2nd whorls (respectively). When a specimen has 6 stamens, it can be assign to the appropriate genus (*Endiandra* or *Beilschmiedia*) by looking at the position of the stamens in the floral whorls. Stamens of *Endiandra* are in the 2nd and 3rd whorls whereas those of *Beilschmiedia* are in the 1st and 2nd whorls.

It is noted that characters selected for creating for phylogenetic analysis were highly subjective. The tree topology is determined largely by characters selected for the analysis. Different characters used for the phylogenetic analysis, the tree topology resulted from the analysis will be different. In this study, *Endiandra* and *Beilschmiedia* were polyphyletic when some characters, position of stamens characters (Character 36–38), were excluded. Inclusion of characters indicating position of stamens separated *Endiandra* and *Beilschmiedia*. Similarly, different sets of characters used for grouping will result in different grouping systems depending on the importance of characters chosen. Difficulties in finding a good set of characters for grouping occurred also in the family *Lauraceae* in general, for examples Pax (1889) used the number of anther locules to delimit the subfamilies and it is noted that such character did not have a generic value (Rohwer 1993).

CONCLUSION

It is concluded that based on the phylogenetic analysis of morphological characters, *Endiandra* are grouped into several clades, however grouping within *Endiandra* based on the presence and absence of staminal glands is not well supported. Moreover, based on morphological characters in this analysis, the monophyly of *Endiandra* and *Beilschmiedia* cannot be confirmed. Different characters used for the phylogenetic analysis will result different tree topologies. Important characters for separating the two genera are number of stamens and position of stamens in the floral whorls.

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REFERENCES

Arifiani D. 2001. Taxonomic revision of *Endiandra* (*Lauraceae*) in Borneo. *Blumea* 46: 99–124.

Armstrong JE & Irvine AK. 1990. Functions of staminodia in beetle-pollinated flowers of *Eupomatia laurina*. *Biotropica* 22: 429–431.

Blume CL. 1850. *Museum Botanicum Lugd.- Bat* 1: p. 270.

Brown R. 1810. *Prodromus Florae Novae Hollandiae et Insulae Van Diemen*. Typis Richardi Taylor et Socii, London.

Chanderbali AS, Werff H van der & Renner SS. 2001. Phylogeny and historical biogeography of *Lauraceae*: Evidence from the chloroplast and nuclear genomes. *Annals of Missouri Botanical Garden* 88: 1044–134.

Felsenstein J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* 39: 783–791.

Hyland BPM. 1989. A revision of *Lauraceae* (excluding *Cassytha*). *Austral. Syst. Bot.* 2: 135–367.

Kitching IJ, Forey PL, Humphries CJ & Williams DM. 1998. *Cladistics, Theory and Practice of Parsimony Analysis* (Second Edition). Oxford University Press.

Kochummen KM. 1989. *Lauraceae*. In: Ng FSP (ed.). *Tree Flora of Malaya*, Vol. 4. Longman, Malaysia.

Kostermans AJGH. 1957. *Lauraceae*. *Reinwardtia* 4(2): 193–256.

Kostermans AJGH. 1969. Materials for a revision of *Lauraceae* II. *Reinwardtia* 7: 451–536.

Li J & Christophel DC. 2000. Systematic relationships within the *Litsea* complex (*Lauraceae*): A cladistic analysis on the basis of morphological and leaf cuticle data. *Australian Systematic Botany* 13: 1–13.

Meissner. 1864. *Lauraceae*. In: De Candolle (ed.). *Prodromus Systematis Naturalis Regni Vegetabilis*.

Mez C. 1889. *Lauraceae* Americanae. *Jargb. Konigl. Bot. Gard. Berlin* 5: 1–556.

Nees von Esenbeck FCGD. 1831. In: Wallich, *Pl. Asiat. Rar.* 2: 61, 69. London

Nishida S. 2001. Notes on *Beilschmiedia* (*Lauraceae*) of Southeast Asia1: Checklist of the Bornean species with the Description of a new species. *Acta Phytotax. Geobot.* 52: 103–113.

Nishida S. 2008. Taxonomic revision of *Beilschmiedia* (*Lauraceae*) in Borneo. *Blumea* 53: 345–383.

Pax F. 1889. *Lauraceae*. In: Engler A and Prantl K. (eds.), *Die Naturlichen Pflanzenfamilien*, Vol. III. 2, Leipzig.

Rohwer JG. 1993. *Lauraceae*. In: Kubitzki K, Rohwer JG & Bittrich V. (eds.). *The Families and Genera of Vascular Plants II*. Springer Verlag, Berlin.

Rohwer JG. 2009. The timing of nectar secretion in staminal and staminodial glands in *Lauraceae*. *Plant Biology*: 1–3.

Swofford DL. 1998. *PAUP*: Phylogenetic Analysis Using Parsimony*. Sunderland, Massachusetts: Sinauer Associates.

Teschner H. 1923. *Die Lauraceen Nordost-Neu-Guineas*. *Engl. Bot. Jahrb. Syst.* 58: 413–420.

Welzen van PC, Slik JWF & Alahuhta J. 2005. Plant Distribution patterns & Plate Tectonics in Malesia. *Biol. Skr* 55: 199–217.

Werff H van der & Richter HG. 1996. Toward an improved classification of *Lauraceae*. *Annals of Missouri Botanical Garden* 83: 409–18.

Werff H van der. 2001. An annotated key to the genera of *Lauraceae* in the Flora Malesiana region. *Blumea* 46: 125–140.