



Problem in the generic delimitation between *Alseodaphne*, *Dehaasia* and *Nothaphoebe* (*Lauraceae*) in Borneo

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Key words

Alseodaphne
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Abstract *Alseodaphne*, *Dehaasia* and *Nothaphoebe* are, morphologically, three closely related genera belonging to the *Persea* subgroup of the *Lauraceae*. A total of 214 binomials of the three genera have been published by various authors (International Plant Names Index, March 2007), of which 44 have been attributed to species occurring in Borneo. In revising the *Lauraceae* for the Tree Flora of Sabah and Sarawak Project, we recognize 40 distinct species (i.e., *Alseodaphne* 11; *Dehaasia* 16; and *Nothaphoebe* 13) for Sabah and Sarawak. These include 34 previously known and 6 undescribed species. Despite many attempts by various authors (Rohwer 1993, 2000, Van der Werff & Richter 1996, Van der Werff 2001) to clarify the generic delimitation between these three genera, to date there remains to be no satisfactory solution. In the absence of a well-accepted generic delimitation and classification within the *Lauraceae* as a whole, and for the purpose of preparing revision of the *Lauraceae* for the Tree Flora of Sabah and Sarawak, we have opted for recognising *Alseodaphne*, *Dehaasia* and *Nothaphoebe* as distinct genera. The distinguishing morphological characters of these three genera, based on specimens from Borneo (Sabah and Sarawak, in particular) are presented.

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INTRODUCTION

The *Lauraceae* is one of the largest and important families of trees and shrubs throughout tropical and subtropical forests. About 2 500–3 000 species in 50 genera estimated worldwide consist of many species that are important ecologically and economically (Kostermans 1957, Hutchinson 1964, Burkill 1966, Rohwer 1993, Van der Werff & Richter 1996).

Based on literature dating back to Blume (1825), about 287 species in 16 genera of the *Lauraceae* have been reported for Borneo. All these 16 genera are represented in Sabah and Sarawak. At local level, the revision of the *Lauraceae* for Sabah and Sarawak is still on-going. To date, we recognise 208 species in 16 genera of *Lauraceae* in Sabah and Sarawak, of which 11 represent undescribed new species.

In the past, many authors have proposed various generic and suprageneric classifications within the *Lauraceae*. Various morphological and anatomical characters (Miquel 1858, Bentham 1880, Hooker 1886, Pax 1889, Kostermans 1957, 1968, 1973a, b, Hutchinson 1964, Rohwer 1993, Christophel et al. 1996, Van der Werff & Richter 1996, Van der Werff 2001) as well as selected molecular markers (Rohwer 2000, Chanderbali et al. 2001, Li et al. 2004) have been used to classify and re-classify the genera. As a result, several genera have repeatedly been recognised as distinct or reduced to the synonymy of other genera and placed under similar or different suprageneric groups and/or subgroups within *Lauraceae*. For example, Miquel (1858), Bentham (1880) and Kostermans (1957) included *Nothaphoebe* in *Persea* Mill. while Hooker (1886), Boerlage (1900), Van der Werff (2001) reduced it to *Alseodaphne*. On the other hand, Bentham (1880), Pax (1889) and Hutchinson (1964) considered *Alseodaphne* as a synonym of *Persea* but Hooker (1886), Boerlage (1900),

Gamble (1912), Ridley (1924) and Kostermans (1973a) recognised *Alseodaphne* and *Persea* as two distinct genera.

The problem in generic delimitation within the *Lauraceae* is not confined to the above mentioned three genera but also prevails in the so-called *Laurus/Litsea*-group ('Laureae') represented in Borneo by *Actinodaphne* Nees, *Iteadaphne* Blume, *Lindera* Thunb., *Litsea* Lam., *Neolitsea* (Benth.) Merr. (Rohwer 1993, Van der Werff 2001, Li et al. 2004, Ng 2005).

In the absence of a well-accepted suprageneric classification and generic delimitation for the *Lauraceae* as a whole, botanists involved in the revision of the *Lauraceae* for the Tree Flora of Sabah and Sarawak volume, have adopted the generic delimitation as proposed by Van der Werff (2001), except for the inclusion of *Nothaphoebe* within *Alseodaphne*.

Alseodaphne, *Dehaasia* and *Nothaphoebe* are morphologically closely similar genera belonging to the *Persea* subgroup of the *Ocotea* group of the *Lauraceae*. Other genera occurring in Borneo that have been placed in the same subgroup include *Persea*, *Phoebe* Nees and *Caryodaphnopsis* Airy Shaw (Rohwer 1993).

The genus *Alseodaphne* was established by Nees (1831) with *A. semecarpifolia* Nees as the type species. Since then, a total of 98 binomials have been published by various authors (International Plant Names Index 2007). Of these, 11 apply to species occurring in Borneo (Kostermans 1973a). The present study discovered three more entities representing undescribed taxa from Sabah and Sarawak (Yahud et al. in prep.).

Dehaasia was first described by Blume (1836) with *D. microcarpa* Blume (i.e., synonym for *D. incrassata* (Jack) Kosterm.) as the type species (Kostermans 1973b). A total of 52 binomials have been published for the genus (International Plant Names Index 2007). Of these, seven were attributed to species occurring in Borneo while other species listed in International Plant Names Index (2007) were without indication that the species occurred in Borneo. Kostermans (1973b) recognised 35 species in the genus, distributed from China to New Guinea. Of these, 14 were reported from Borneo. In the present study (Yahud &

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Table 1 Comparison between *Alseodaphne*, *Dehaasia* and *Nothaphoebe* based on readily observable vegetative and reproductive characters.

Character / Species	<i>Alseodaphne</i> (Fig. 1; Plate 1a, d)	<i>Dehaasia</i> (Fig. 2; Plate 1b, e)	<i>Nothaphoebe</i> (Fig. 3; Plate 1c, f)
Terminal (vegetative) bud	Not or rarely perulate	Not perulate	Not perulate
Leaves			
arrangement	Alternate or sub-opposite	Alternate	Alternate or opposite
texture	Usually crowded at the end of twig, sometimes not crowded	Crowded at the end of twig or rarely not crowded	Loosely or closely crowded at the end of twig
indumentum on lower surface	Coriaceous	Coriaceous or pubescent	Coriaceous or chartaceous
colour of lower surface	Glabrous or pubescent	Glabrous or pubescent	Glabrous, sparsely pubescent or glabrescent
size (cm)	Glabrous or not	Glabrous or not	Usually not glaucous or sometimes glaucous
midrib upper surface	(6–)10–32(–52) by (2–)4.5–13(–21)	(4.5–)10–40(–60) by (2–)3–10(–21)	(2.8–)4–26.5(–33) by (1.5–)3–10(–11.5)
lateral veins upper surface	Flat, sunken or raised	Flat, sunken or raised	Raised or flat
intercostal veins	Usually flat, sometimes sunken or raised	Usually flat, sometimes sunken or raised	Usually raised, sometimes flat or sunken
	Reticulate, areolate or scalariform	Reticulate, areolate or scalariform	Reticulate or scalariform
Petiole			
axial side	Channelled throughout	Channelled but rounded at the base	Rounded or indistinctly channelled
length (cm)	1–5(–7)	1–2.5(–5)	(0.3–)1–2(–3)
diameter (mm)	1–5	1–2.2(–4)	1–2(–3)
position of inflorescence	Usually terminal, sometimes axillary or extra-axillary	Terminal or extra-axillary	Usually extra-axillary, sometimes axillary or terminal
number of flowers per inflorescence	Few, occasionally many	Few	Many
lateral flowers of terminal cymes	Not opposite	Strictly opposite	Strictly opposite
relative length of inflorescence compared to leaves	Usually longer, rarely shorter or as long as leaves	Shorter or as long as leaves	Usually shorter than leaves or rarely longer than leaves
length of proximal rachis (axis) before 1st branching (cm)	2–15	(1–)2–10(–11.5)	(<i>N. heterophylla</i>)
number of flowers on the distal part of inflorescence	3	2–3	0.5–5, rarely 11 (<i>N. heterophylla</i>)
size of outer perianth lobes	Usually smaller or almost equal, rarely larger than the inner ones	Smaller or almost equal as the inner ones	3–5, rarely 2
3rd whorls with a pair of glands	Yes	Yes	Slightly smaller than the inner ones
glands	Sessile or stalked	Sessile	Sometimes not
number of anther locules	4, rarely 2 (<i>A. oblanceolata</i>)	2	Usually sessile, sometimes shortly stalked
arrangement of pollen sacs	In 2 pairs above each other, rarely side by side	Side by side	4
shape	Ovoid or oblong	Ovoid, obovoid, oblong or rounded	In 2 pairs above each other
Filaments			Oblong or obovoid, rarely ovoid
relative length	Usually shorter, sometimes longer or as long as anthers	Usually longer, sometimes shorter or as long as anthers	Usually shorter than anther or anther sessile, rarely as long as anthers
Filament of staminodes			Absent or very short
shape	Distinct	Distinct	Triangular
Pistil			
ovary	Triangular or rarely club-shaped	Club-shaped, subulate or triangular	Ovoid, globose or ellipsoid
length of style compared to ovary	Globose, ovoid, obovoid or ellipsoid	Globose or ovoid	Usually longer, sometimes shorter or as long
stigma	Usually shorter, sometimes longer or as long	Longer or shorter than ovary	Peltate or discoid
Fruits	Peltate, discoid or heart-shaped	Peltate or discoid	
shape	Rounded, rounded-ellipsoid, ellipsoid, oblong or obovoid	Obovoid, ellipsoid, oblong or rounded	Ellipsoid, obovoid or oblong
receptacle shape	Usually shallow saucer-shaped or rarely flat	Usually flat or rarely shallow saucer-shaped	Flat
receptacle diameter (mm)	3–18	2–12	(3–)5–8(–12)
receptacle texture	Usually fleshy or rarely woody	Fleshy	Woody
persisting perianth lobes (mm)	2–8 by 2–12	1–10 by 2–12	2–4 by 2–6
Pedice			
texture	Usually fleshy or rarely woody	Usually fleshy or rarely woody	Woody
shape	Distinctly swollen	Usually distinctly swollen or rarely indistinctly thickened	Usually indistinctly thickened or sometimes not thickened
colour when fresh	Usually bright red or red, rarely pale green	Reddish or red	Pale brown or brown
width of top of pedicel (mm)	(3–)4–8(–38)	2–5(–15)	(3–)5–9(–13)

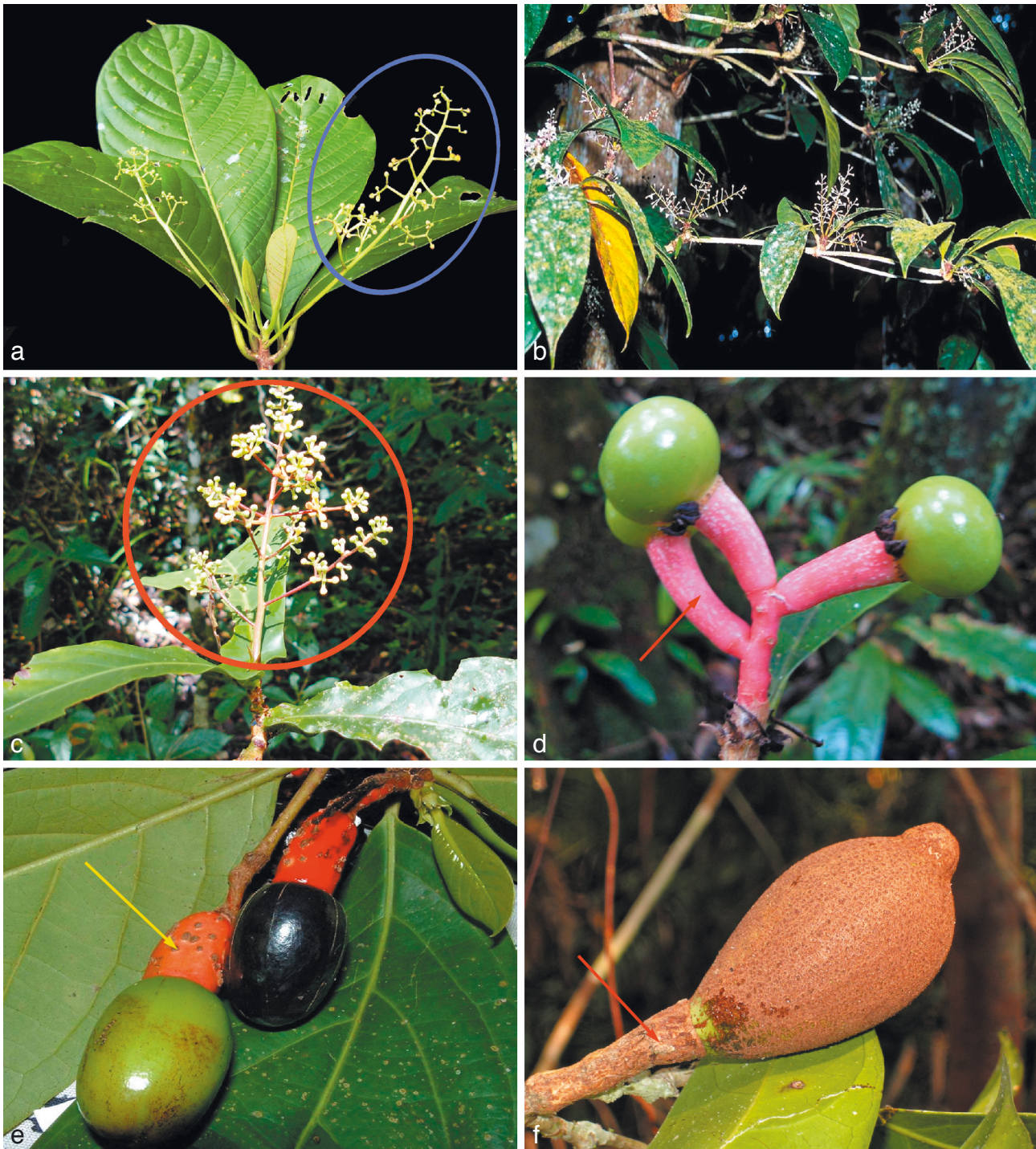


Plate 1 a. Inflorescence of *Alseodaphne elmeri*; b. inflorescence of *Dehaasia brachybotrys*; c. inflorescence of *Nothaphoebe sarawakensis*; d. fruit and pedicel of *Alseodaphne borneensis*; e. fruit and pedicel of *Dehaasia incrassata*; f. fruit and pedicel of *Nothaphoebe havilandii*. © TFSS Project.

Soepadmo in prep.) we recognise 16 species in Sabah and Sarawak, including two new species.

The genus *Nothaphoebe* was established by Blume (1851) with *N. umbelliflora* (Blume) Blume (basionym: *Ocotea umbelliflora* Blume) as the type species. A total of 45 binomials have been published (International Plant Names Index 2007), of which only two apply to species found in Borneo. Present revision (Julia et al. in prep.) recognises 13 species in Sabah and Sarawak including four new species to be described.

As has been adequately discussed by Rohwer (1993, 2000), Van der Werff (2001) and Li et al. (2004), hitherto, the suprageneric classification as well as the generic delimitation within the *Lauraceae* are largely remain unresolved. Some of the main reasons for this problem are the lack of recent and

up-to-date revisions and/or monographs of most of the known genera and that classification based mainly on morphological and anatomical evidence is generally inconclusive and unsatisfactory. The problem is compounded further by the fact that only a few genera have been subjected to molecular studies (e.g., Chanderbali et al. 2001, Li et al. 2004).

This paper is a first report following from a study undertaken by the authors as part of the revision of *Lauraceae* for the Tree Flora of Sabah and Sarawak Project (Julia et al. in prep., Yahud & Soepadmo in prep., Yahud et al. in prep.). Its main goal is to highlight the readily observed morphological characters which may be used to distinguish and identify species of *Alseodaphne*, *Dehaasia* and *Nothaphoebe* occurring in Sabah and Sarawak.

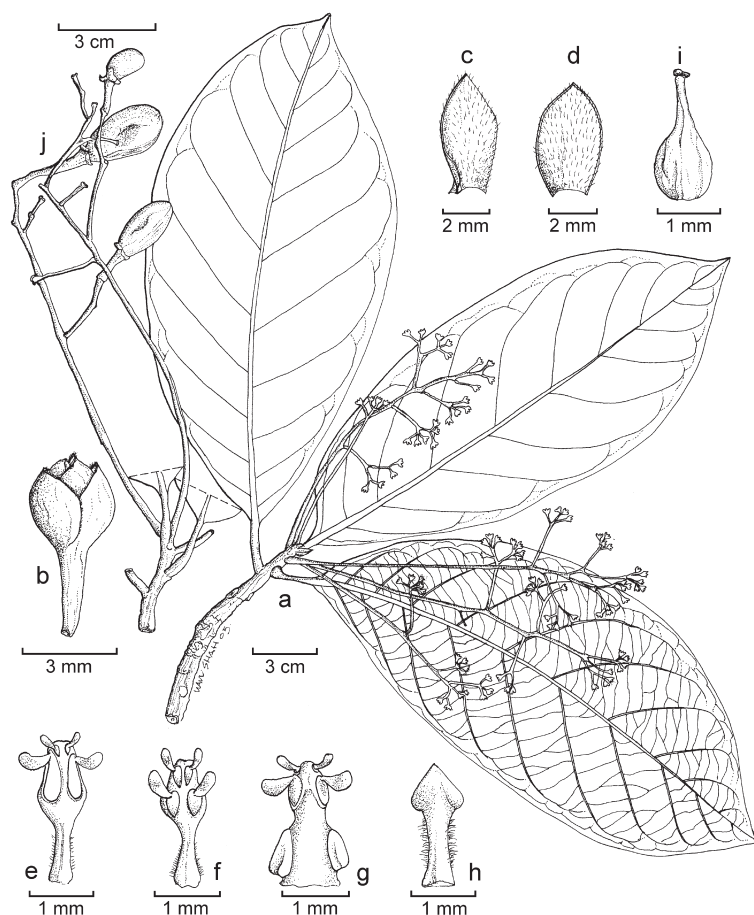


Fig. 1 *Alseodaphne elmeri* Merr. a. Flowering leafy twig; b. flower bud; c, d. outer and inner perianth lobes; e. first whorl stamen; f. second whorl stamen; g. third whorl stamen with a pair of glands; h. staminode; i. ovary; j. infructescence (a–i: *Elmer* 21164, j: *S* 23946). © TFSS Project.

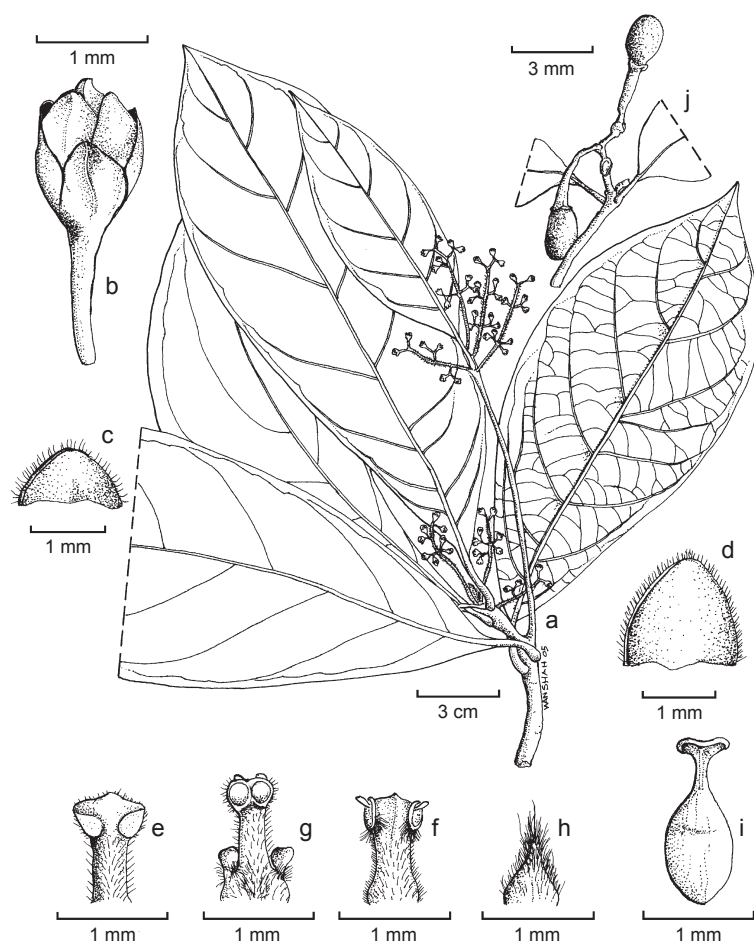


Fig. 2 *Dehaasia turfosa* Korsterm. a. Flowering leafy twig; b. flower bud; c, d. outer and inner perianth lobes; e. first whorl stamen; f. second whorl stamen; g. third whorl stamen with a pair of glands; h. staminode; i. ovary; j. infructescence (a–i: *S* 9262, j: *Haviland* 3090). © TFSS Project.

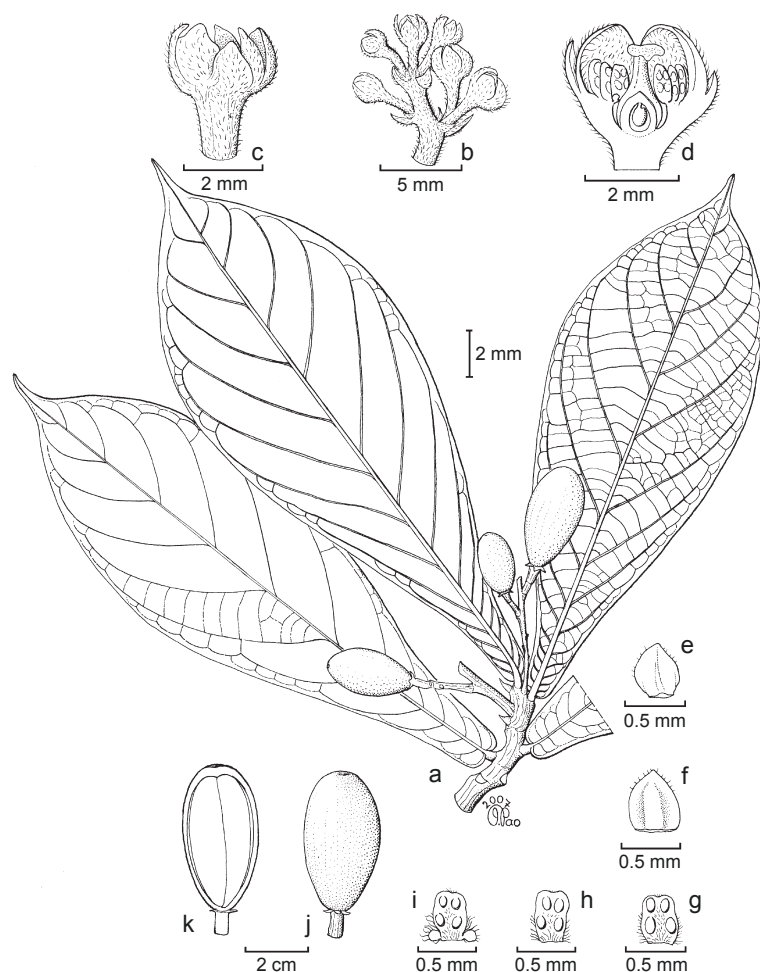


Fig. 3 *Nothaphoebe sarawakensis* Gamble. a. Fruiting leafy twig; b. terminal/distal part of inflorescence; c. flower bud; d. longitudinal section of flower bud; e. outer perianth lobe; f. inner perianth lobe; g. first whorl stamen; h. second whorl stamen; i. third whorl stamen with a pair of glands; j. fruit; k. longitudinal section of fruit (a: S 60316, b–i: S 83384; j, k: S 34612). © TFSS Project.

MATERIAL AND METHODS

A total of about 1 500 herbarium specimens of *Alseodaphne*, *Dehaasia* and *Nothaphoebe* collected from Borneo (particularly in Sabah and Sarawak) and its adjacent islands were investigated at the herbaria of the Forest Research Institute Malaysia (KEP), Forest Research Centre, Sandakan, Sabah (SAN), Sabah Parks (KNP), Forest Research Centre, Kuching, Sarawak (SAR), Singapore Botanical Garden (SING), Herbarium Bogoriense (BO) and the Philippines National Herbarium (PNH). Digital images of type specimens were obtained from the websites made available online by The National Herbarium of the Netherlands, University of Leiden Branch (L), The New York Botanical Gardens (NY) and The Royal Botanic Gardens Kew (K). Additional flowering and fruiting specimens were occasionally obtained from the field in Sabah and Sarawak.

RESULT AND DISCUSSION

Comparative morphology of Alseodaphne, Dehaasia and Nothaphoebe in Borneo

We selected vegetative and reproductive characters which were comparable and readily observable on the herbarium specimens (Table 1).

Table 1 shows that none of the selected vegetative characters can be used conclusively to distinguish the three genera. On the other hand, a number of characters of the petiole, inflorescence, flower and fruit can, in combination, be utilized to large extent to segregate the three genera. In the past, one or more of the characters mentioned in Table 1 were used by previous authors to identify or distinguish these three genera (e.g., leaves

arrangement, colour of lower surface, lateral flowers of terminal cymes, perianth lobes, glands, number of anther locules, arrangement of pollen sacs, filament staminodes, receptacle, fruits and fruit pedicels). Sometimes these characters were used to classify the genera into subfamilies in *Lauraceae*; in addition, like many authors before, we are still using more or less similar characters of the inflorescences and fruits to distinguish these genera. Nevertheless, additional characters that we find useful to distinguish *Alseodaphne*, *Dehaasia* and *Nothaphoebe* include: 1) the number of flowers per inflorescence; 2) relative length of inflorescence compared to the length of leaves; 3) length of proximal rachis (axis) before the first branching; and 4) the number of flowers on the distal part of inflorescence. At this stage and for the revision of these three genera for the Tree Flora of Sabah and Sarawak, we tried to use as many characters as possible to distinguish these genera; however, since we only look at Borneo specimens, variation in the characters across these three genera are possible particularly when one study the genera worldwide.

Morphological similarity and differences between the three genera

Based on our experience dealing with specimens from Borneo, particularly those collected from Sabah and Sarawak, the characters presented in Table 1 can be used to distinguish *Alseodaphne*, *Dehaasia* and *Nothaphoebe* with some degree of certainty; however, since the differences are mainly based on inflorescences and fruits characters, identification of sterile materials are still quite impossible unless one is familiar with all the species in the genera.

Similarity — All three genera normally have non-perulate terminal vegetative buds. The leaves are pinnately veined and usually crowded at the end of the upright twig. The texture of the leaf blade varies between species across the three genera even though species of *Nothaphoebe* generally have smaller and thinner leaf blade compared to those of *Alseodaphne* and *Dehaasia*. All three genera have a thyrsopaniculate inflorescence known as Type II by Van der Werff (2001); bisexual and trimerous flowers with 6 perianth lobes arranged in 2 whorls (with the lobes of the outer whorl are smaller than or equal to that of the inner ones), 9 fertile stamens arranged in 3 whorls, 3 staminodes, and ovary seated on a flat or shallow hypanthium (receptacle); and the fruit is 'unprotected', subtended only by a shallow saucer-shaped or flat receptacle.

Differences — Data presented in Table 1 suggest that, except for the number of anther locules (4 vs 2), *Alseodaphne* is more similar to *Dehaasia* than to *Nothaphoebe*. This finding is conform with the suggestion made by Rohwer (1993) but contradicts Van der Werff's (2001) proposal in which *Nothaphoebe* is treated as a synonym of *Alseodaphne*.

For the purpose of identifying the genera/species occurring in Borneo (Sabah and Sarawak in particular), the comparative morphological data presented in this paper suggest that the three genera can be distinguished as follows:

Nothaphoebe differs from both *Alseodaphne* and *Dehaasia* in its rounded or adaxially only indistinctly channelled petiole; many-flowered inflorescence with shorter proximal axis, distal part with 3–5 flowers, filament of fertile stamen very short or absent, more or less sessile staminodes, woody fruit-receptacle with smaller persisting perianth lobes, woody and not or only slightly thickened brown or pale brown fruit-pedicel.

Most species of *Alseodaphne* can be distinguished from that of *Dehaasia* by combination of the following characters: lateral flowers of terminal cymes non-opposite (vs strictly opposite); anther 4-locular (vs mostly 2-locular), except in *Alseodaphne oblaneolata* with 2-locular anther; fruiting receptacle mostly shallow saucer-shaped (vs mostly flat), except in *Alseodaphne borneensis* with flat receptacle. In the case whereby one odd character is observed, combinations of majority of the characters take precedence over the single character.

CONCLUSION

As discussed above, *Alseodaphne*, *Dehaasia* and *Nothaphoebe* can be distinguished by a combination of characters. To certain extent, some of these characters are rather qualitative and argumentative, nevertheless for the above and more pressing practical reasons, botanists involved in the revision of the *Lauraceae* for the Tree Flora of Sabah and Sarawak have, with a minor exception, adopted the generic delimitation as proposed by Van der Werff (2001). In this context, we have opted to recognize *Alseodaphne*, *Dehaasia* and *Nothaphoebe* as three distinct genera.

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