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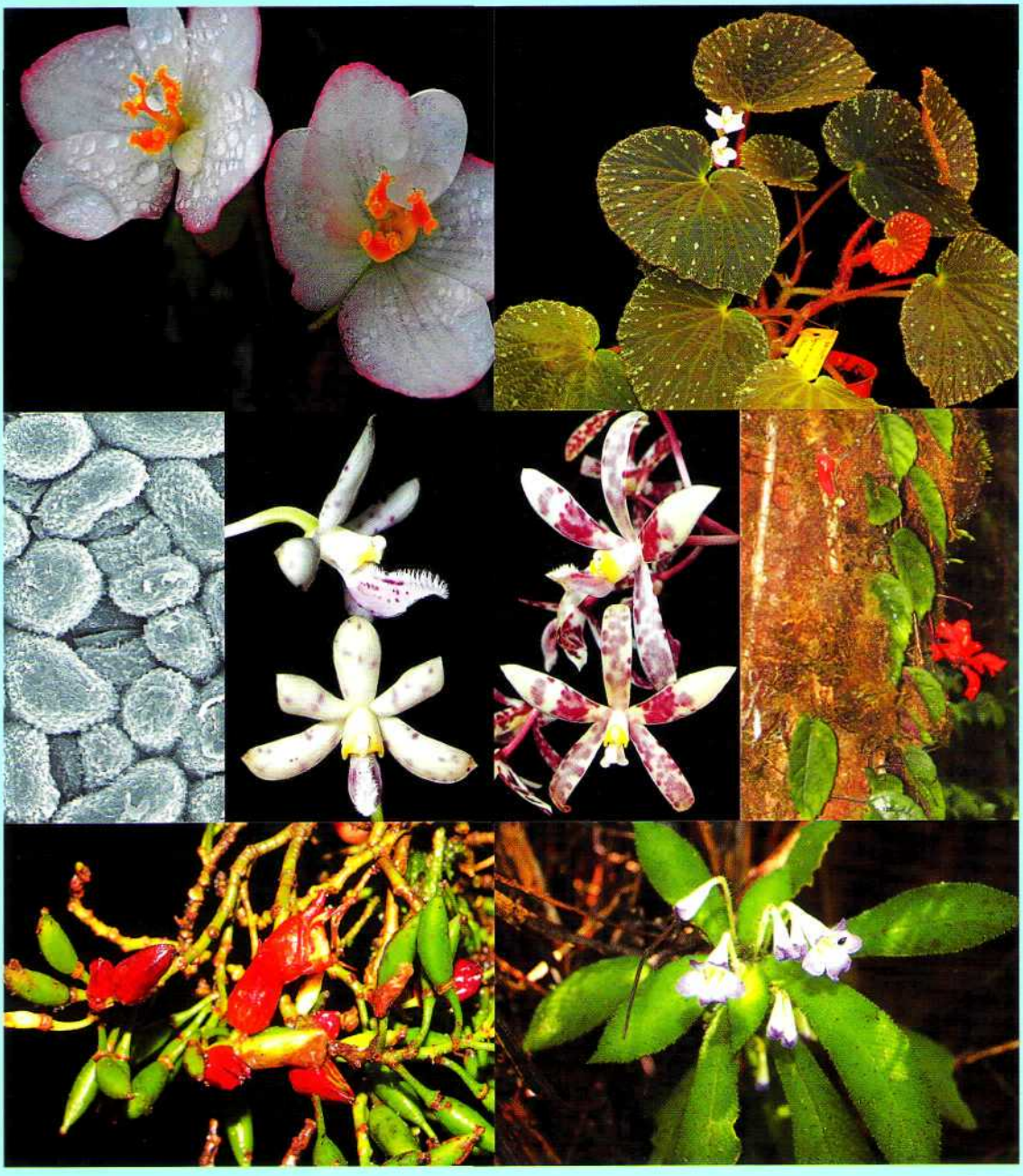

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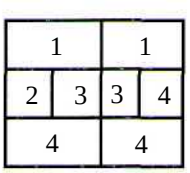

Cover images: 1. *Begonia holosericeoides* (female flower and habit) (Begoniaceae; Ardi *et al.); 2.* Abaxial cuticles of *Alseodaphne rhododendropsis* (Lauraceae; Nishida & van der Werff); *3. Dipodium puspitae, Dipodium purpureum* (Orchidaceae; O'Byrne); 4. *Agalmyla exannulata, Cyrtandra coccinea* var. *celebica, Codonoboea kjellbergii* (Gesneriaceae; Kartonegoro & Potter).

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DO CUTICLE CHARACTERS SUPPORT THE RECOGNITION OF ALSEODAPHNE, NOTHAPHOEBE & DEHAASIA AS DISTINCT GENERA?

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ABSTRACT
NISHIDA, S. & VAN DER WERFF, H. Do cuticle characters support the recognition of *Alseodaphne, Nothaphoebe* and *Dehaasia* as distinct genera? *Reinwardtia* 14(1): 53 – 66. ― The Asian members of the *Persea* group are divided among the genera *Alseodaphne*, *Apollonias*, *Dehaasia*, *Machilus*, *Nothaphoebe* and *Phoebe*. A recent phylogenetic analysis has shown that *Machilus* and *Phoebe* are supported as monophyletic genera but evidence that the closely related genera *Alseodaphne*, *Dehaasia* and *Nothaphoebe* are monophyletic or not was equivocal. In this study we analyzed cuticle characters of 95 collections belonging to the Asian members except for *Apollonias*. We anticipated two possible outcomes. If the genera were not monophyletic, we expected that the groups based on cuticle characters would consist of species belonging to different genera. If the genera were monophyletic, we expected that the groups based on cuticle characters would consist of species belonging to the same genus. We found 16 groups based on cuticles. Of these, 12 consisted of species of a single genus (one group included a single species and thus a single genus). The four mixed groups included mostly species of one genus with 1 or 2 species of a different genus. Our results support the recognition of *Alseodaphne*, *Dehaasia*, *Machilus*, *Nothaphoebe* and *Phoebe* as distinct genera.

Key words: *Alseodaphne*, cuticle, *Dehaasia*, Lauraceae, *Machilus*, *Nothaphoebe.*

ABSTRAK
NISHIDA, S. & VAN DER WERFF, H. Apakah karakter kutikula mendukung pengenalan *Alseodaphne*, *Nothaphoebe* dan *Dehaasia* sebagai marga yang berbeda? *Reinwardtia* 14(1): 53 – 66. ― Kelompok *Persea* dari Asia dibedakan menjadi beberapa marga yaitu *Alseodaphne*, *Apollonias*, *Dehaasia*, *Machilus*, *Nothaphoebe* dan *Phoebe*. Hasil analisis kekerabatan menunjukkan bahwa *Machilus* dan *Phoebe* adalah marga yang monofili, namun tidak demikian halnya dengan tiga marga yang berkerabat dekat yaitu *Alseodaphne*, *Dehaasia* dan *Nothaphoebe*. Pada studi ini telah dianalisis karakter kutikula dari 95 koleksi yang termasuk dalam kelompok Asia kecuali *Apollonias* dengan dugaan dua hasil yang telah diantisipasi. Pertama, jika marga-marga tersebut tidak monofili, maka pengelompokan yang didasarkan pada karakter kutikula pada jenis-jenis tersebut berasal dari marga yang berbeda. Kedua, jika marga-marga tersebut monofili maka pengelompokan yang didasarkan pada karakter kutikula jenis-jenis tersebut berasal dari marga yang sama. Dari hasil studi ditemukan 16 kelompok berdasarkan karakter kutikulanya. Dua belas kelompok terdiri atas jenis-jenis yang berasal dari satu marga (satu kelompok terdiri atas satu jenis yang berarti satu marga juga). Sedangkan empat kelompok yang bercampur termasuk jenis-jenis yang berasal dari satu marga dengan satu atau dua jenis dengan marga yang berbeda. Hasil studi ini mendukung pengenalan *Alseodaphne*, *Dehaasia*, *Machilus*, *Nothaphoebe* dan *Phoebe* sebagai marga yang berbeda.

Kata kunci: *Alseodaphne*, kutikula, *Dehaasia*, Lauraceae, *Machilus*, *Nothaphoebe.*

INTRODUCTION

The *Persea* group as currently accepted consists of seven genera, *Alseodaphne* Nees, *Apollonias* Nees, *Dehaasia* Blume, *Machilus* Nees, *Nothaphoebe* Blume, *Persea* Mill. and *Phoebe* Nees and includes 400–450 species (Li *et al*., 2011). The group is well represented in subtropical and tropical America, is absent from Africa and Madagascar and has a large number of species in subtropical and tropical Asia. No members of this group are known from Australia nor the Pacific area. All Neotropical species are placed in *Persea* (*ca*. 80 species), *Apollonias* consists of one species in the Canary Islands and one in India, while the remaining genera range from Pakistan to Japan and south to New Guinea. *Machilus* (*ca*. 100 species) and *Phoebe* (100 species fide Li *et al.*, 2008, but *ca*. 50 species fide Kochummen, 1989) have their centers of diversity in southern China. *Alseodaphne* (50 sp. or more), *Nothaphoebe* (40 sp.) and *Dehaasia* (35 sp.) are most common in tropical Asia with only few species in southern China.

Modern treatments for Asian members of these

genera are few or lacking. Regional treatments of *Machilus* and *Phoebe* are published in the Flora of China (Li *et al*., 2008), covering the majority of the species of these genera. Kostermans published synopses of *Alseodaphne* (1973a) in which he recognized 50 species and of *Dehaasia* (1973b) with 35 species. These synopses consist of descriptions of new species, listing of accepted species with citation of specimens, but do not include keys to species. There is no recent treatment of *Nothaphoebe* (*ca*. 40 sp.).

Morphologically, the Asian genera of the *Persea* group are poorly defined. No floral differences have been reported between *Machilus* and *Phoebe*; the sole difference is found in the condition of the persistent tepals in fruit and the shape of the fruit: spreading to recurved tepals and round fruits in *Machilus vs*. erect, clasping tepals and ovoid fruits in *Phoebe*. A few species, such as *M. calcicola* Qi or *M. glabrophylla* Zuo, have round fruits and deciduous tepals. A few species placed in *Phoebe* are described as having globose fruits and loose, lax or slightly clasping tepals in fruit (*P. chinensis* Chun, *P. microphylla* H.W. Li, *P. faberi* (Hemsley) Chun; see Li *et al*., 2008). Assigning flowering specimens to either *Machilus* or *Phoebe* remains problematic. The majority or possibly all species of *Machilus* and *Phoebe* have perulate vegetative buds, leaving clusters of scars at the base of the seasonal shoots; *Alseodaphne*, *Nothaphoebe* and *Dehaasia* do not have perulate buds (pers. obs.). There is no consensus on differences between *Alseodaphne* and *Nothaphoebe*. During the last sixty years a variety of opinions have been published. Kostermans (1957) placed *Alseodaphne* and *Nothaphoebe* in *Persea*, but later (Kostermans, 1973a) reconsidered and accepted both as good genera without indicating how they could be separated. In an unpublished treatment of the Lauraceae in Thailand (a copy owned by one of the authors, HvdW) Kostermans separated *Alseodaphne* from *Nothaphoebe* based on the fruiting pedicels: thick and fleshy in *Alseodaphne*, cylindrical and not fleshy in *Nothaphoebe*. This manuscript was probably written in the early 1970's. Kostermans also identified many collections in L; he placed nearly all specimens with unequal tepals in *Nothaphoebe* and those with equal or subequal tepals in *Alseodaphne* (pers. obs.). Kochummen (1989) treated species with unequal tepals in *Nothaphoebe* and species with subequal tepals in *Alseodaphne*. Rohwer (1993) separated the two by the size of the staminodes of whorl four: *Alseodaphne* was said to have well-developed, heart-shaped staminodes and *Nothaphoebe* small staminodes. Van der Werff (2001) included *Nothaphoebe* in *Alseodaphne*. Most recently, Julia *et al*. (2009) studied *Alseodaphne* and *Nothaphoebe* for the Tree Flora of Sabah and Sarawak; they separated the two genera on a variety of characters (petioles canaliculate *vs*. rounded, few-flowered *vs*. many-flowered inflorescences, distinct *vs*. very short or absent filaments of the fertile stamens and fleshy *vs*. woody fruiting pedicels). *Dehaasia* is generally considered to be closely related to *Alseodaphne* and *Nothaphoebe*, differing only in the number of pollen sacs per anther, *Alseodaphne* and *Nothaphoebe* being 4-locular and *Dehaasia* 2-locular (Kostermans, 1973b; Rohwer, 1993; van der Werff, 2001). Fruiting specimens therefore cannot be identified to genus with any confidence and Kochummen (1989) already deplored the description of new species based solely on fruiting specimens. The lack of recent revisions with keys to species makes even identification of flowering specimens difficult and this lack of reliable identifications poses large problems for studies of relationships in this group.

Two recent studies have presented phylogenetic analyses of the *Persea* group (Rohwer *et al*., 2009; Li *et al*., 2011). The phylogenies found in these studies are not identical, however, these studies share a number of conclusions. The main ones referring to Asian members are the following: *Machilus* is a monophyletic group and separate from *Persea*; *Persea* is not monophyletic and consists of a large group (mostly of subg. *Eriodaphne*) and a small group (mainly subg. *Persea*), plus (sometimes) a few species currently placed in *Alseodaphne*; *Phoebe* is not monophyletic in Rohwer *et al*. (2009), but monophyletic in Li *et al*. (2011); *Alseodaphne* is not monophyletic, but consists of two groups; *Dehaasia* is nested in one of the *Alseodaphne* groups and *Nothaphoebe* was only represented by one species which was part of the *Alseodaphne*/*Dehaasia* group.

In our study we focused on characters of the cuticles found in the Asian *Persea* group. Cuticular characters are features of the cutinized epidermal cells or stomatal complex. They have been long used in identifying fossil leaves (*e.g*. Upchurch, 1984a, 1984b; Carpenter *et al*., 2010) and investigating relationships among extant taxa (Baranova, 1972, 1987, 1992; Stace, 1984; Yang & Lin, 2005). Observation of cuticles requires relatively simple methodology. One can use fresh or dried specimens for cuticle studies, including material that is not suitable for molecular analyses. Sterile specimens might also provide useful information for classification, which cannot be expected for conventional Lauraceae systematics that usually requires some reproductive characters.

We analyzed cuticle characters of 95 collections

belonging to the Asian members except for *Apollonias*. We anticipated two possible outcomes. If the genera were not monophyletic, we expected that the groups based on cuticle characters would consist of species belonging to different genera. If the genera were monophyletic, we expected that the groups based on cuticle characters would consist of species belonging to the same genus.

MATERIALS AND METHODS

Cuticles of 95 leaf samples of *Persea* complex were examined (Appendix 1). All were from Asian countries (Cambodia, China, Malaysia, Indonesia, Philippines, Thailand and Vietnam), and included species of *Alseodaphne*, *Dehaasia*, *Machilus*, *Notaphoebe*, and *Phoebe* (one species of *Persea*, which should belong to *Machilus* was also included). Leaves were collected from herbarium specimens at MO and L, using one leaf sample per species. Identities (genus names, species names, localities or collector's names) of the plant samples were not known to the first author who examined the cuticles before her grouping them by the cuticular characters.

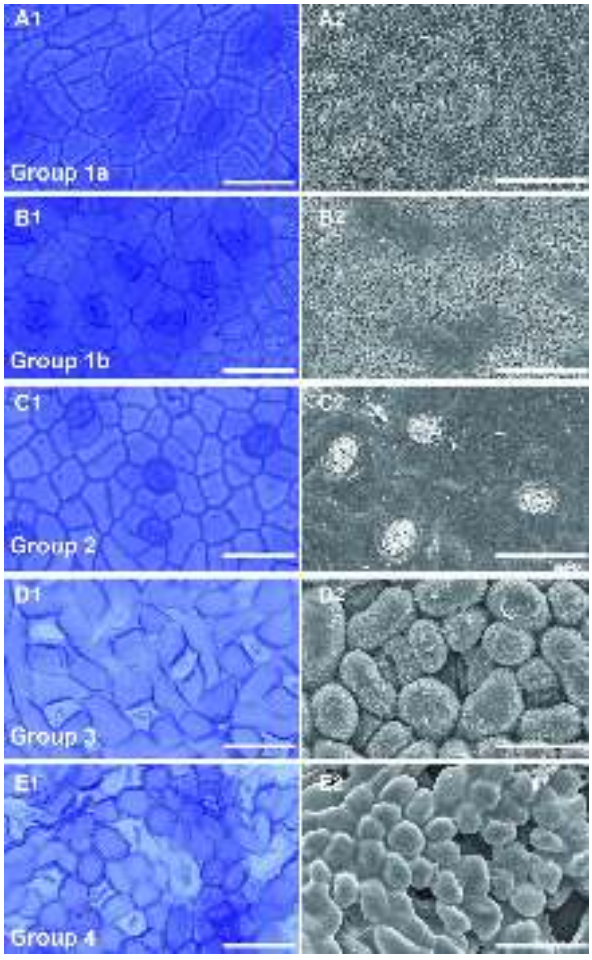

Fig. 1. Optical micrographs of the abaxial cuticles (A_1, B_1, C_1, D_1, E_1) and SEMs of the stomatal complex (A_2, B_2, C_2, D_2, E_2). A. *Alseodaphne* sp. 7; B. *Alseodaphne* sp. 10; C. *Alseodaphne* sp. 15; D. *Alseodaphne rhododendropsis*; E. *Phoebe lucida*. Scale bars = 50 μm.

The examination procedure basically followed that of Christophel *et al*. (1996), Nishida and Christophel (1999), and Nishida and van der Werff (2007). A 1 cm square sample was taken from left basal part of the leaf (with the adaxial surface up) for each species. The leaf samples were soaked in 90% ethanol overnight then placed in a test tube with *ca*. 2 mL 30% H_2O_2 and *ca*. 1 mL 90% ethanol. The test tubes were heated around 100°C in a heated dry block bath for about 3 hr. When the samples turned soft and yellow, they were placed in a Petri dish with tap water, tenderly cleaned with a fine artist's brush to remove the cellular contents or leaf veins, then placed in bottles with 90% ethanol for more than one night. Each sample was then rinsed in 2% ammonia (to adjust the pH), transferred to a Petri dish with tap water to clean with a fine artist's brush once more. The cuticles were stained in 0.1% crystal violet for *ca*. 1 min., then mounted in phenol glycerin jelly on a slide, covered with an 18 mm square cover glass and observed under an optical microscope. Feature descriptions follow Christophel *et al*. (1996), Nishida and Christophel (1999), or Nishida and van der Werff (2007, 2011). All the cuticles (except for three species, *Dehaasia* sp. 1, *Machilus* sp. 10, and *Phoebe formosana*, whose cuticles were fragile and broke apart during the preparation) were also examined using an SEM. Sample preparation was the same as described above. Samples were dehydrated in a t-butanol series (90% ethanol : t-butanol = 3:1; 1:3; 100% t-butanol twice), freeze-dried using a JFD-310 (JEOL, Tokyo, Japan) at -5°C, then coated with platinum, and observed under a JSM-6060B microscope (15 kV; JEOL).

Without being informed about the identity (the genus or species names, the locality, or the reproductive characters), one of the authors (Nishida) observed cuticles firstly only under optical microscope and grouped samples by their overall similarity of the cuticles. SEM was not available at the time. We later reexamined cuticles with SEM, and reconsidered the groups if the characters under SEM were largely different from the previous impression we had under optical microscope.

Because generic concepts have varied from author to author, we give below the generic characters we have used. *Machilus* and *Phoebe* are separated on their fruit characters, *Machilus* with reflexed or spreading tepals and round fruits, *Phoebe* with clasping tepals and ovoid fruits; *Dehaasia* is characterized by its 2-locular stamens

and *Alseodaphne* and *Nothaphoebe* are separated on their tepals; unequal tepals in *Nothaphoebe* and equal tepals in *Alseodaphne*.

RESULTS

Among the 95 samples, two samples (*Alseodaphne peduncularis* and *A*. sp. 16) were excluded from the results because cuticles were not well removed from leaf tissue and unobservable. Cuticular features were different between the adaxial and abaxial leaf surfaces; stomata were observed only on the abaxial leaf surfaces. Features consistent within each of the samples but varied among the species were observed mainly on the abaxial leaf surfaces. They are listed in Table 1, and samples with the representative features are shown in Figs. 1-4. Drawings of the cuticle parts or features we refer to (and may be difficult to understand from the sample pictures) are shown in Figs. 5-7. The following are brief descriptions of the features.

In many species, periclinal walls of epidermal cells or stomatal complex (Fig. 5) were smooth (Figs. $2B_2$, $2C_2$, $2D_2$, $3B_2$, $3C_2$), or granular (*e.g.* Figs. $1A_2$, $1B_2$, $1D_2$, $2A_2$, $3D_2$, $3E_2$, $4A_2$). The structures mentioned here as "granular" may be remains of epicuticular waxes, but we used the term because the appearance of them under microscope resembled the ones referred to as granular by Christophel & Rowett (1996). Epidermal cells were sometimes papillose or strongly protruding upward (Figs. $1D_2$, $1E_2$, $2E_2$, $3A_2$), although surface of the papillae or the protruding cells themselves could be smooth (Figs. $1E_2$, $2E_2$) or granulous (Fig. $1D_2$, $3A_2$). Peri-

Table 1. Cuticle character states recognized for the Asian *Persea* genera.

Part of cuticle	Characters	Character states
Epidermal anticlinal walls	Straightness of walls	straight to slightly curved / with loose U-shaped curves / with tight U-shaped curves
Epidermal periclinal walls	Surface texture*	smooth / weakly granulous / granulous
	Surface appearance*	flat / each cell protruding upward / papillose
Stomatal complex	Overall shape*	narrowly rectangular / elliptic / broadly elliptic / (hidden under papillae or protrusion of epidermal cells)
	Stainability of subsidiary cells	stained as much as epidermal cells / darkly stained / inner part scarcely stained but outer part darkly stained
	Lower ledges*	lip-shaped / butterfly-shaped
	Surface appearance*	almost flat / irregularly protruding / circular and protruding / reniform and protruding / lip-shaped and protruding / dome-shaped and protruding / (hidden among protrusion or papillae of epidermal cells)
	Surface texture*	smooth /granulous

* Characters used for the grouping.

clinal walls were usually homogeneous within each sample, but in some species they were different between the cells surrounding stomata and the other part of the epidermal cells (Fig.1B_2): the former had granulous periclinal walls, whereas the other part had smooth ones. A few species had only their subsidiary cells with granulous periclinal walls (Fig. 1C_2).

Anticlinal walls of epidermal cells were usually straight to slightly curved, and sinuous anticlinal walls were rarely seen. Straightness of anticlinal walls of subsidiary cells made the stomatal overall shape (Fig. 6) different: usually the walls were curved outward and the stomatal complexes look elliptic to broadly elliptic (Fig. 6A; *e.g.* Fig. 2B_1), but in a few cases they were straight and the stomatal complexes look narrowly rectangular (Fig. 6B; Figs.1A_1, 1B_1, 4A_1).

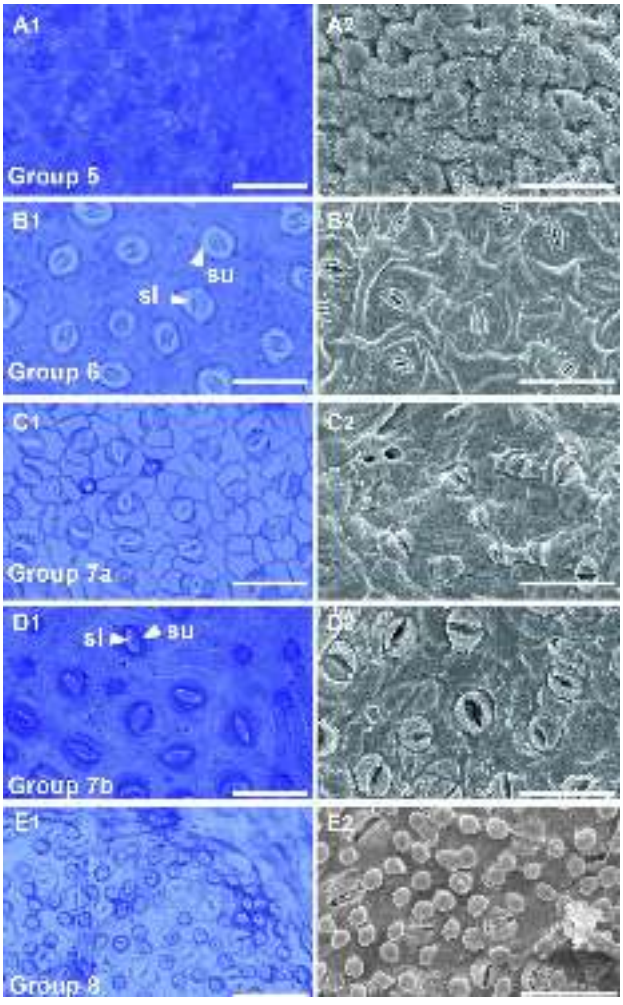

Fig. 2. Optical micrographs of the abaxial cuticles (A_1, B_1, C_1, D_1, E_1) and SEMs of the stomatal complex (A_2, B_2, C_2, D_2, E_2). A. *Alseodaphne insignis*; B. *Nothaphoebe sarawacensis*; C. *Phoebe neurantha*; D. *Alseodaphne andersonii* (*#Poilane 19847*); E. *Nothaphoebe cavalieriei*. sl = stomatal ledges. su = subsidiary cells. Scale bars = 50 μm.

Stomatal ledges (the most inside part of the stomatal complex and along the stomatal opening slit; Fig. 5) are usually stained only weakly (*e.g.* "sl" of Figs. 2B_1 and 2D_1), but other part of the complex, which mainly consists of subsidiary cells, may have their periclinal walls stained by crystal violet. If the entire periclinal walls are stained only weakly (*e.g.*, "su" of Fig. 2C_1), darkly (*e.g.* "su" of Fig. 2D_1), or only outer edge of the walls stained darkly (*e.g.* "su" of Fig. 2B_1) is observable under the microscope, and we listed the states as dyed patterns of the subsidiary cells (Table 1).

Surface appearance of the stomata recognized under SEM had some variation: almost flat and inconspicuous (Fig. 7A; Figs.1A_2, 1B_2, 3D_2, 3E_2), irregularly protruding (Fig. 7B; Fig. 4A_2), circular and protruding (Figs. 1C_2, 3A_2, 3B_2, 3C_2), reniform and protruding (Fig. 7C; Fig. 2A_2), lip-shaped and protruding (Fig. 7D; Fig. 2B_2), dome-shaped and protruding (Fig. 7E; Figs. 2C_2, 2D_2, 2E_2). In the

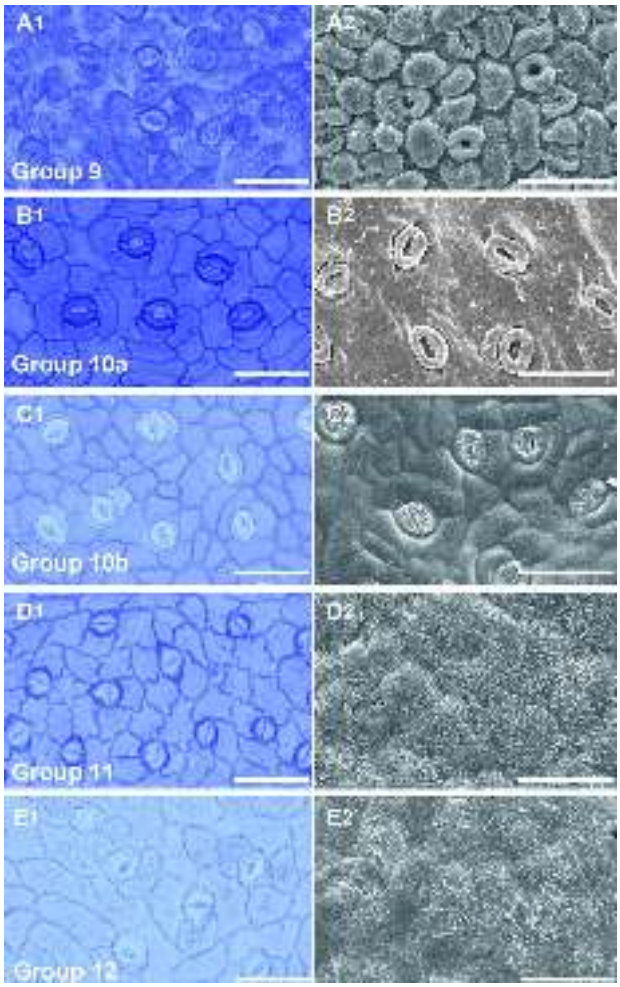

Fig. 3. Optical microgaphs of the abaxial cuticles (A_1, B_1, C_1, D_1, E_1) and SEMs of the stomatal complex (A_2, B_2, C_2, D_2, E_2). A. *Machilus kurzii*. B. *Alseodaphne* sp. 8. C. *Dehaasia* sp. 4. D. *Dehaasia cairocan*. E. *Dehaasia* sp. 3. Scale bars = 50 μm.

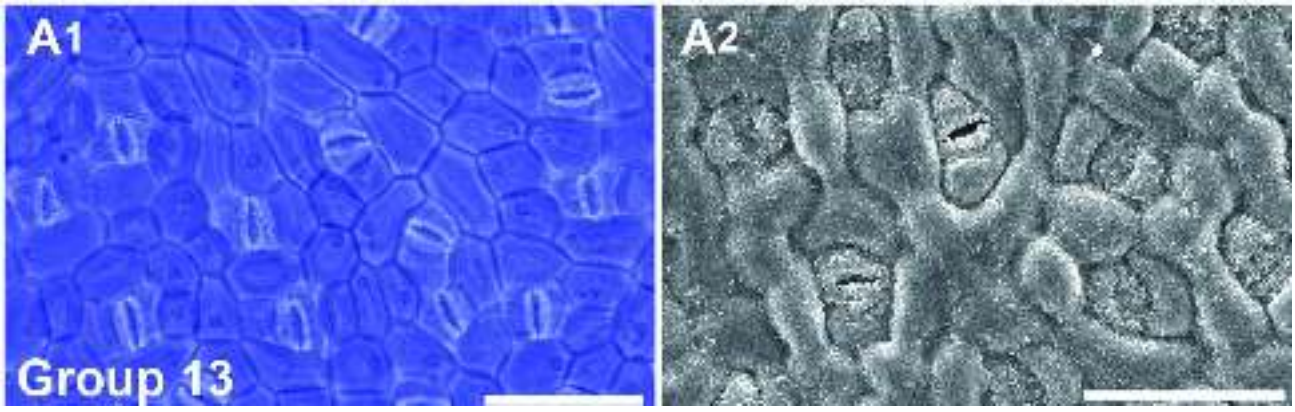

Fig. 4. Optical micrographs of the abaxial cuticles (A_1) and SEMs of the stomatal complex (A_2). A. *Alseodaphne* sp. 12. Scale bars = 50 μm.

cuticle of circular and protruding stomatal surface, circles may appear perfect (Fig. 7F; Fig. $3B_2$) or broken at both ends of the stomatal slit (Fig. 7G; Fig. $3A_2$, $3C_2$). Differences among circular surface, lip-shaped surface and dome-shaped surface were relative width of the complex (length of the complex crossing the stomatal slit perpendicularly) and shape of the part near the stomatal slit: the width was usually as long as or longer than the slit in the circular shaped surface or dome shaped surface but shorter than the slit in the lip shaped surface; the part near the stomatal slit was slightly depressed in the circular shaped surface or lip shaped surface whereas it was protruding in the dome shaped surface. In some species, stomatal complexes were hidden under the papillae of the epidermal cells or protruding surface of the surrounding epidermal cells (Figs. $1D_2$, $1E_2$). As we mentioned in the description of the periclinal walls, some species had only the stomatal complex with granulous periclinal

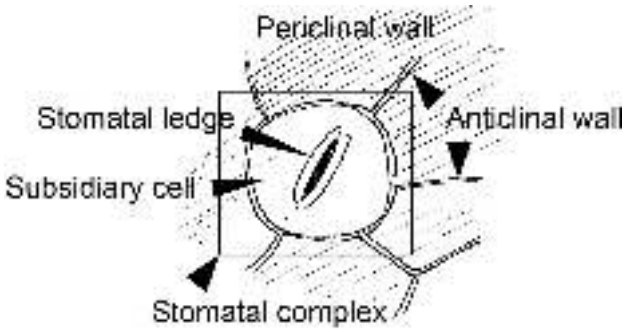

Fig. 5. Diagram of a typical stomatal complex of the Asian *Persea* group.

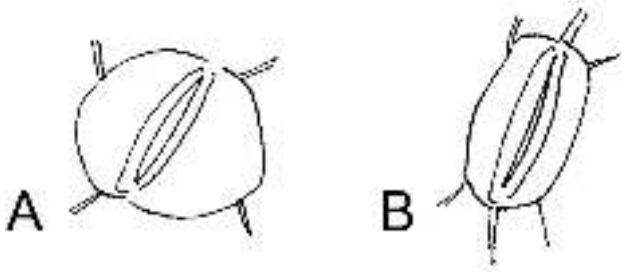

Fig.6. Overall shape of the stomatal complex in the Asian *Persea* group. A. Elliptic to broadly elliptic. B. Narrowly rectangular.

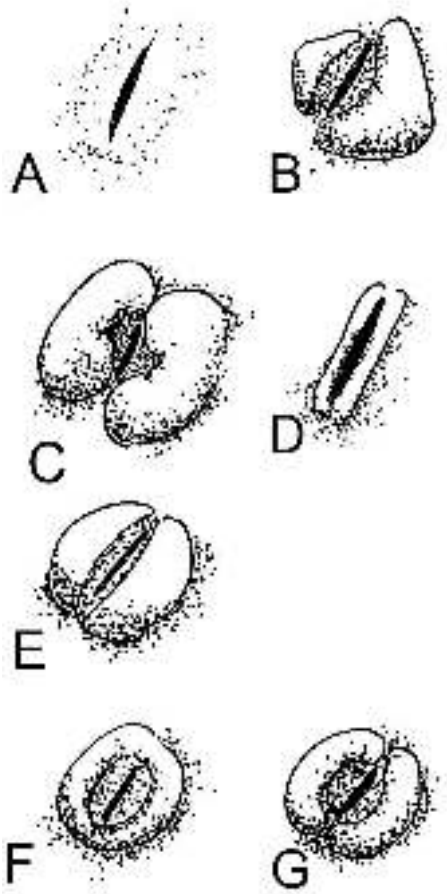

Fig. 7. Stomatal surface appearance patterns of the Asian *Persea* group. A. Almost flat. B. Irregularly protruding. C. Reniform and protruding. D. Lip-shaped and protruding. E. Dome-shaped and protruding. F. Circular and protruding, with the circle perfect. G. Circular and protruding, with the circle broken at both ends of the stomatal slit.

walls (Fig. $1C_2$) or stomatal complex and epidermal cells surrounding the stomata with granulous walls (Fig. $1B_2$).

DISCUSSION

We found 16 groups based on cuticles (Table 2, 3). If groups share the same number (*eg*. 1a and 1b) this indicates that their cuticles appear more similar to each other than to the other groups. Names of species that have exceptional features and are only tentatively placed in one of the groups are placed in parentheses in the table. These species must be further investigated to examine their attribution. As we mentioned in Materials and Methods, we firstly observed the cuticles under optical microscope and grouped the species, then later reexamined with SEM and reconsidered the groups if the characters observed under SEM were largely different from the previous impression we had with optical microscope. This way, seven of our 93 samples (*#Hyland 14931* of *Alseodaphne andersonii*, *A. glaucina*, *A.* sp. 14, *Dehaasia* sp. 3, *Phoebe neurantha* and *P. formosana*, *P. tavoyana*) were moved to a different group.

The cuticular characteristics used for the grouping mainly belong to the stomatal complex, but the features of the periclinal walls were also used. As mentioned earlier (Nishida and van der Werff 2011), features of the stomatal complex might be better correlated with molecular phylogeny than features of epidermal cells, and we also considered the former ones more important. In the key to the groups (Table 3), however, we used features of the epidermal cells more often, because they are more easily recognized. Dyed patterns of the stomatal complex (whether subsidiary cells are stained darkly or not) might be a new character recognized for cuticular studies of Lauraceae.

Twelve of the 16 groups consist of species of a single genus (including one group with just a single species). The four mixed groups included mostly species of one genus with 1 or 2 species of a different genus. Because the taxonomy of the genera is poorly known, it is very well possible that the mixed groups are a consequence of misidentifications. For example, the species identified as *Nothaphoebe cavaleriei* is a species of *Phoebe* and the specimen identified as *Alseodaphne* sp. 13 has unequal tepals and is thus a species of *Nothaphoebe*. Our results, therefore, support the recognition of *Alseodaphne*, *Dehaasia*, *Machilus*, *Nothaphoebe* and *Phoebe* as distinct genera. Most of the species were grouped by the first author without their generic or distributional information, which indicates the groupings were not biased by such information. This suggests that the cuticular characters might be useful to recognize some natural taxa, if we use the characters carefully. We, of course, still have a problem to rely on the cuticles. For instance, the groupings were based on the overall similarity of the features and without any quantification. It was hard to quantify features like the appearance of the stomatal complex, but we need some systems of the cuticular characters that are more accessible and easier to recognize even for non-specialists. More objective ways of evaluation of the features, including more comparison with the other morphologies or molecular phylogeny, are also needed.

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Table 2. Groupings of species of the Asian *Persea* group by cuticular characters.

Group	Species name	Surface appearance and texture of abaxial leaf epidermis and stomata	Overall shape of stomata	Stainability of subsidiary cells	Lower stomatal ledges	Surface appearance of stomata
1a	*Alseodaphne elongata*, *A.* sp. 6, *A.* sp. 7, *A.* sp. 9	granulous	narrowly rectangular	darkly stained	lip-shaped	almost flat
1b	(*Alseodaphne hainanensis*), *A. glaucina*, *A.* sp. 10, *A.* sp. 14.	cells around stoma granulous, other cells smooth	narrowly rectangular	darkly stained	lip-shaped	almost flat
2	(*Alseodaphne obovata)*, *A.* sp. 5, *A.* sp. 15.	subsidiary cells granulous, other cells smooth	broadly elliptic	darkly stained	lip-shaped	circular and slightly protruding
3	*Alseodaphne rhododendropsis*, *A.* sp. 1, *A.* sp. 2.	granulous, each cell protruding upward	hidden under epidermis	scarcely stained	lip-shaped	hidden under epidermis
4	*Phoebe lucida*, *P. macrophylla*, *P.* sp. 1, *P.* sp. 2.	papillose (papilla surface smooth)	hidden under papillae	scarcely stained	lip-shaped	hidden under epidermis
5	*Alseodaphne insignis*, *A. oblanceolata*	slightly granulous	broadly elliptic	darkly stained	butterfly-shaped	reniform and protruding
6	*Notaphoebe cuneata*, *N. sarawacensis*, *N.* sp. 1, *N.* sp. 2, *Alseodaphne* sp. 13[*1]	smooth	broadly elliptic	only outer part darkly stained	lip-shaped	lip-shaped and protruding
7a	(*Phoebe neurantha*), *P. formosana*, *P. lanceolata*, (*Machilus* sp. 1)	smooth	broadly elliptic	weakly stained	lip-shaped	dome-shaped and protruding
7b	*Alseodaphne andersonii*, *A.* sp. 3	almost smooth	broadly elliptic	darkly stained	lip-shaped	dome-shaped and protruding
8	*Nothaphoebe cavalieri*[*2], *Phoebe bourneri*, *P. cathia*, *P. chekiangensis*, *P. forrestii*, *P. hunanensis*, *P. sheareri*, *P. tavoyana*, *P.* sp. 4	each cell papillose or strongly protruding upward (papillae surface smooth)	broadly elliptic	weakly stained	lip-shaped	dome-shaped and protruding

Table 2. Groupings of species of the Asian *Persea* group by cuticular characters (continued).

9	*Alseodaphne* sp. 4., *Machilus bombycina*, *M. breviflora*, *M. calcicola*, *M. chekiangensis*, *M. decursinervis*, *M. gamblei*, *M. glabrophylla*, *M. grandibracteata*, *M. grijsii*, *M. kurzii*, (*M. minutiloba*), *M. nakao*, *M. odoratissima*, *M. oreophila*, *M. parabreviflora*, (*M. phoenics*), *M. platycarpa*, *M. pomifera*, *M. velutina*, *M.* sp. 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, *Persea rimosa*, (*Phoebe* sp. 3)	granulous, each cell usually protruding upward	broadly elliptic	scarcely stained	lip-shaped	circular and protruding, circles broken at the both ends of the stomatal slit
10a	*Alseodaphne* sp. 8, 11[*3]	smooth	elliptic	darkly stained	lip-shaped	circular and protruding, circles perfect
10b	*Dehaasia turfosa*, *D.* sp. 1, 2, 4, (6), *(Persea chatacea*)[*4]	smooth	elliptic	scarcely stained	lip-shaped	circular and slightly protruding, circles almost perfect
11	(*Alseodaphne semecarpifolia*), *Dehaasia annamensis*, *D. cairocan*, (*D. suborbicularis*)	granulous	broadly elliptic	only outer part darkly stained	lip-shaped	flat to slightly irregularly protruding
12	(*Dehaasia tomentosa*), *D.* sp. 3, 5.	granulous	broadly elliptic	scarcely stained	lip-shaped	almost flat
13	*Alseodaphne* sp 12.	slightly granulous	narrowly rectangular	scarcely stained	lip-shaped	irregularly protruding

Species temporally placed in the group in parentheses.
[*1] *Alseodaphne* sp. 13 should belong to *Nothaphoebe* based on floral morphology (van der Werff, unpublished).
[*2] *Nothaphoebe cavalerieri* should belong to *Phoebe* based on ITS-based phylogeny (Rohwer *et al*., 2009) and general morphology (van der Werff, p. 200 in Li *et al*, 2008).
[*3] The two samples, which were named as *Alseodaphne* sp. 8 and *A.* sp. 11, came from the same tree, one collection with flowers, the other with fruits.
[*4] This species should belong to *Machilus* based on floral morphology (van der Werff, unpublished).

Table 3. Key to the cuticular groupings.

1a. All or a part of abaxial leaf epidermis (including stomatal complex) with granulous walls, whether the cells protruding upward or not 2
b. All of abaxial epidermis with smooth periclinal walls or papillose (pallila surface smooth) 10

2a. Only abaxial epidermal cells surrounding stoma with granulous periclinal walls 3
b. All the abaxial epidermal cells with granulous walls 4

3a. Subsidiary cells and epidermal cells surrounding the subsidiary cells with granulous periclinal walls; stomatal surface almost flat ..... Group 1b
b. Only subsidiary cells with granulous periclinal walls; stomatal surface circular and slightly protruding (Fig. 7G) ..... Group 2

4a. Stomatal surface reniform (Fig. 7C) and protruding; stomatal ledges butterfly-shaped ..... Group 5
b. Stomatal surface almost flat to slightly protruding, but not reniform; stomatal ledges lip-shaped 5

5a. Stomatal surface circular and protruding ..... Group 9
b. Stomatal surface almost flat, irregularly protruding or hidden under epidermis 6

6a. Epidermal cells protruding conspicuously upward, with stomatal surface (subsidiary cell surface) hidden under the epidermal cells ..... Group 3
b. Epidermal cells flat or only slightly protruding, with stomatal surface (subsidiary cell surface) visible, whether it is flat or protruding 7

7a. Subsidiary cells narrowly rectangular, with the outer anticlinal walls almost straight (Fig. 6B) 8
b. Subsidiary cells broadly elliptic, with the outer anticlinal walls curved outward (Fig. 6A) 9

8a. Stomatal surface almost flat ..... Group 1a
b. Stomatal surface irregularly protruding ..... Group 13

9a. Outer part of subsidiary cells darkly stained, making a contrast with the inner part of the subsidiary cells that are scarcely stained ..... Group 11
b. Outer part of subsidiary cells stained only weakly as the inner part ..... Group 12

10a. Stomatal surface (subsidiary cell surface) hidden under papilla ..... Group 4
b. Stomatal surface protruding 11

11a. Stomatal surface lip-shaped and protruding (Fig. 7D), with width of the protrusion usually shorter than the stomatal slit ..... Group 6
b. Stomatal surface circular or dome-shaped and protruding, with width of protrusion usually as long as or longer than the stomatal slit 12

12a. Stomatal surface dome shaped and protruding, with the part near stomatal slit also protruding 13
b. Stomatal surface circular and protruding, with the part near stomatal slit slightly depressed 15

13a. Epidermal cells papillose or strongly protruding upward ..... Group 8
b. Epidermal cells scarcely or only weakly protruding 14

14a. Outer part of subsidiary cells only weakly stained ..... Group 7a
b. Outer part of subsidiary cells stained darkly ..... Group 7b

15a. Rim of the circular stomatal surface darkly stained and conspicuous under optical microscope ..... Group 10a
b. Rim of the circular stomatal surface scarcely stained and inconspicuous under optical microscope ..... Group 10b

Appendix 1. List of the samples examined. Specimens are deposited in MO or L.

Species	Specimen no.	Locality
Alseodaphne andersonii (King) Kosterm.	Poilane 19847	Vietnam
Alseodaphne andersonii (King) Kosterm.	Hyland 14931	China
Alseodaphne elongate (Blume) Kosterm.	de Wilde 18784	Indonesia
Alseodaphne glaucina (A.Chev.) Kosterm.	Chevalier 38873	Vietnam
Alseodaphne hainanensis Merr.	Yu 103147	China
*Alseodaphne insignis*Gamble	Mohtar S 54836	Sarawak
Alseodaphne oblanceolata (Merr.) Kosterm.	SAN 35191	Indonesia
Alseodaphne obovata Kosterm.	Ashton 5823	Indonesia
Alseodaphne peduncularis Hook.f.	Rahmat 2980	Indonesia
Alseodaphne rhododendropsis Kosterm.	Poilane 3566	Vietnam
Alseodaphne semecarpifolia Nees	Bernardi 15385	Ceylon
Alseodaphne sp. 1	van der Werff 23932	Vietnam
Alseodaphne sp. 2	van der Werff 23889	Vietnam
Alseodaphne sp. 3	van der Werff 23855	Vietnam
Alseodaphne sp. 4	van der Werff 17084	Vietnam
Alseodaphne sp. 5	Lee S 45516	Sarawak
Alseodaphne sp. 6	Mohtar S 59461	Sarawak
Alseodaphne sp. 7	Jamree S 73282	Sarawak
Alseodaphne sp. 8	Maxwell 07-702	Thailand
Alseodaphne sp. 9	Garcia 15942	Philippines
Alseodaphne sp. 10	Gaerlan 26377	Philippines
Alseodaphne sp. 11	Maxwell 06-515	Thailand
Alseodaphne sp. 12	Julaihi S 83465	Sarawak
Alseodaphne sp. 13	Julaihi S 83482	Sarawak
Alseodaphne sp. 14	Wu WP 409	Vietnam
Alseodaphne sp. 15	Enjah S 81836	Sarawak
Alseodaphne sp. 16	de Wilde 20304	Indonesia
Dehaasia annamensis Kosterm.	Poilane 2786	Vietnam
Dehaasia cairocan (S.Vidal) C.K.Allen	Curran 10392	Philippines
Dehaasia suborbicularis (Lecomte) Kosterm.	Poilane s.n.	Vietnam
Dehaasia tomentosa (Blume) Kosterm.	Kostermans 4896	Indonesia
Dehaasia turfosa Kosterm.	SAR 9268	Indonesia
Dehaasia sp. 1	Arifiani 37	Indonesia
Dehaasia sp. 2	de Wilde 15572	Indonesia
Dehaasia sp. 3	Kessler 2130	Indonesia
Dehaasia sp. 4	de Wilde 14420	Indonesia
Dehaasia sp. 5	Adriansyah AA 2476	Indonesia
Dehaasia sp. 6	Kessler 303	Indonesia

Appendix 1. List of the samples examined. Specimens are deposited in MO or L (continued).

Species	Specimen no.	Locality
Machilus bombycina King	Maxwell 02-155	Thailand
Machilus breviflora Hemsl.	Wang 37282	China
Machilus calcicola S.Lee & C.J.Qi	Guo 80136	China
Machilus chekiangensis S.K.Lee	Cheng 170507	China
Machilus decursinervis Chun	Chen 14184	China
Machilus gamblei King	Wang 39173	China
Machilus glabrophylla J.F.Zuo	China Germany T 618	China
Machilus grandibracteata S.K.Lee & F.N.Wei	Zhou 10355	China
Machilus grijsii Hance	Huang 161402	China
Machilus kurzii King	Maxwell 13971	Thailand
Machilus minutiloba S.K.Lee	Zhang 5346	China
Machilus nakaoi S.K.Lee	Hou 72073	China
Machilus odoratissima Nees	Middleton 643	Cambodia
Machilus oreophila Hance	Chen 23180	China
Machilus parabreviflora H.T.Chang	Tsang 23803	China
Machilus phoenicis Dunn	He 15100	China
Machilus platycarpa Chun	Wang 38678	China
Machilus pomifera (Kosterm.) S.K.Lee	Wang 34302	China
Machilus velutina Champ.	Guangdong 73 T 2980	China
Machilus sp. 1	Harder 4179	Vietnam
Machilus sp. 2	Harder 4775	Vietnam
Machilus sp. 3	van der Werff 14068	Vietnam
Machilus sp. 4	van der Werff 14104	Vietnam
Machilus sp. 5	van der Werff 14255	Vietnam
Machilus sp. 6	VH 5117	Vietnam
Machilus sp. 7	HAL 111	Vietnam
Machilus sp. 8	Lowry 4918	Vietnam
Machilus sp. 9	Lowry 4921	Vietnam
Machilus sp. 10	van Beusekom 4078	Thailand
Machilus sp. 11	van Beusekom 4793	Thailand
Machilus sp. 12	Poilane 24913	Vietnam
Machilus sp. 13	Poilane 19114	Vietnam
Machilus sp. 14	Chevalier 38790	Vietnam
Machilus sp. 15	Poilane 23288	Cambodia
Machilus sp. 16	Gao 50232	China
Nothaphoebe cavalieriei (H.Lév.) Yang	Xu 527	China
Nothaphoebe cuneata Blume	Kostermans 7103	Indonesia
Nothaphoebe sarawacensis Gamble	Chai S 35449	Sarawak
Nothaphoebe sp. 1	James S 34453	Sarawak
Nothaphoebe sp. 2	Lam 3564	Indonesia
Persea chartacea Kosterm.	Maxwell 00-44	Thailand
Phoebe bournei (Hemsl.) Yang	He 4270	China

Appendix 1. List of the samples examined. Specimens are deposited in MO or L (continued).

Species	Specimen no.	Locality
Phoebe cathia (D.Don) Kosterm.	Maxwell 98-664	Thailand
Phoebe chekiangensis P.T.Li	Ho 30223	China
Phoebe formosana Hayata	Liu 305	Taiwan
Phoebe forrestii W.W.Sm.	Hyland 14912	China
Phoebe hunanensis Hand.-Mazz.	Zuo 859	China
Phoebe lanceolata (Nees) Nees	Maxwell 05-387	Thailand
Phoebe lucida Blume	Beaman 9598	Sabah
Phoebe macrophylla (Nees) Blume	Jacobs 4572	Indonesia
Phoebe neurantha Gamble	Xu 1995119	China
Phoebe sheareri Gamble	Tan 58303	China
Phoebe tavoyana Hook.f.	Hou 70523	China
Phoebe sp. 1	de Vogel 3625	Indonesia
Phoebe sp. 2	Julaihi S 81357	Sarawak
Phoebe sp. 3	Gaoligong SBS 23334	China
Phoebe sp. 4	Gaoligong SBS 22844	China

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