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Alseodaphnopsis (*Lauraceae*) revisited

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Abstract Generic delimitations among the Asian members of the *Persea* group, including the recently described genus *Alseodaphnopsis*, are discussed. These genera, with the exception of *Alseodaphnopsis*, are characterized by reproductive characters. A study of flowers of *Alseodaphnopsis* species found that *Alseodaphnopsis* species have unisexual flowers and that *Alseodaphnopsis* is better defined by its unisexual flowers than by vegetative characters. This is the first report of the presence of unisexual flowers in any member of the *Persea* group.

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ASIAN GENERA OF THE PERSEA GROUP

The classification of the *Lauraceae* has long been problematic. During the 19th century several classifications were proposed (Nees 1836, Meissner 1864, Bentham 1880, Mez 1889), all based on characters of flowers, fruits and inflorescences. During the 20th century Kostermans (1957) added a new scheme, this one largely based on the position of the ovary. Only during the last 40 years have other characters been used in the classification. Richter (1981) proposed a new classification based on his study of wood and bark anatomy; he was the first one to find a close relationship between *Beilschmiedia* Nees and *Cryptocarya* R.Br., two large genera that were in previous classifications widely separated. Van der Werff & Richter (1996) found that three large groups of genera could be recognized on wood and bark anatomy in combination with inflorescence type. More recently DNA based phylogenies (for instance Chanderbali et al. 2001) were found not to be in conflict with the existence of these three main groups of genera with a small number of isolated genera. Following Van der Werff & Richter (1996) we can recognize in tropical Asia three large groups of genera based on morphology:

- the *Beilschmiedia*/*Cryptocarya* group, characterized by paniculate/cymose inflorescences with the lateral flowers of the ultimate cymes not strictly opposite and bisexual flowers with 2-locular stamens;
- the *Litsea* group, characterized by umbellate or pseudo-umbellate inflorescences and unisexual flowers with 2-locular or 4-locular stamens; and
- the *Persea* group sensu Van der Werff & Richter (1996) characterized by paniculate/cymose inflorescences with the lateral flowers of the ultimate cymes strictly opposite and bisexual flowers with 2-locular or 4-locular stamens.

A few small genera present in Asia do not fall into these groups (*Sassafras* J.Presl, *Caryodaphnopsis* Airy Shaw, *Neocinnamomum* H.Liu). Within the three main groups, genera are defined by a variety of floral and fruit characters, such as number of stamens, number of locelli, leaf position, position of the ovary. This system works reasonably well with each genus characterized by a combination of reproductive and/or vegetative characters. One of the three main groups of genera in tropical Asian is the *Persea* group, characterized by the inflorescence type described above. This group consists of the following genera in tropical Asia: *Alseodaphne* Nees, *Cinnamomum* Schaeff. *Dehaasia* Blume, *Machilus* Nees, *Nothaphoebe* Blume and *Phoebe* Nees. The *Persea* group also includes the neotropical *Persea* Mill. and *Apollonias* Nees with one species in the Canary Islands. *Cinnamomum* can be divided into two groups, one with opposite, tripliveined leaves and one with alternate, pinnately to weakly tripliveined leaves with domatia. The other five genera can be separated from *Cinnamomum* by their alternate, pinnately veined leaves without domatia or leaves clustered at the tips of branches and form the focus of this paper. The five Asian members of the *Persea* group have been treated differently by earlier botanists; Kostermans (1957) treated *Machilus*, *Alseodaphne* and *Nothaphoebe* as synonyms of *Persea* and accepted *Dehaasia* and *Phoebe*; Kostermans (1973) recognized *Alseodaphne* and *Nothaphoebe* as distinct genera; Kochummen (1989) accepted *Alseodaphne*, *Dehaasia*, *Nothaphoebe* and *Phoebe*, but treated *Machilus* as a synonym of *Persea*; Van der Werff (2001) recognized *Alseodaphne* (including *Nothaphoebe*), *Dehaasia*, *Persea* (including *Machilus*) and *Phoebe*. Recent DNA based phylogenies (Rohwer et al. 2009, Li et al. 2011) have shown that *Machilus* species and *Phoebe* species form monophyletic groups, that *Machilus* and *Phoebe* should be recognized as distinct genera and that *Persea* is restricted to the New World and Macaronesia. However, the genera *Alseodaphne*, *Dehaasia* and *Nothaphoebe* were poorly represented in the phylogenetic studies and their status remains unresolved. Morphological diagnostic characters separating the five genera are as follows: Both *Machilus* and *Phoebe* have persistent, rather large tepals in the fruiting stage while *Alseodaphne*, *Dehaasia* and *Nothaphoebe* have deciduous tepals or, if tepals are somewhat persistent, they are small and bract-like. *Machilus* and *Phoebe* have very similar flowers and can only be recognized in the fruiting stage. *Machilus* has spreading to reflexed tepals and round fruits while *Phoebe* has erect tepals that clasp the base of the ellipsoid fruits. Diagnostic characters for the other three genera are found in the flowers, not the fruits. *Alseodaphne* has 4-locular stamens and equal tepals, *Nothaphoebe* has 4-locular stamens and unequal tepals (the outer three tepals clearly smaller than the inner three) and *Dehaasia* has 2-locular stamens. *Dehaasia* includes species with equal and unequal tepals. Because the diagnostic characters for *Machilus* and *Phoebe* are only present in the fruiting stage and those for *Alseodaphne*, *Dehaasia* and

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Nothaphoebe only in the flowering stage, assigning specimens to a particular genus remains problematic. Fruiting specimens can be identified to *Machilus*, *Phoebe* or *Alseodaphne*/*Dehaasia*/*Nothaphoebe*; flowering specimens can be identified to *Alseodaphne*, *Dehaasia*, *Nothaphoebe* and *Machilus*/*Phoebe*. Furthermore, floral differences between *Alseodaphne* and *Machilus*/*Phoebe* are not clear; in general *Alseodaphne* has smaller flowers than *Machilus*/*Phoebe*. Due to a lack of DNA samples of reliably identified trees it is not clear if our current concepts of *Alseodaphne*, *Dehaasia* and *Nothaphoebe* correspond with monophyletic groups. Julia et al. (2009) studied the generic distinction between *Alseodaphne*, *Dehaasia* and *Nothaphoebe* and concluded, based on a variety of morphological characters, that all three should be recognized at genus level. Nishida & Van der Werff (2014) studied cuticles of several species of the *Persea* group, including representatives of *Machilus*, *Phoebe*, *Alseodaphne*, *Dehaasia* and *Nothaphoebe*. They recognized a number of groups based on cuticle characters. They anticipated that if the genera were monophyletic, each species group based on cuticle characters would consist of species of one genus and if the genera were not monophyletic, species groups based on cuticle characters would consist of species of more than one genus. They found that the former was the case: species groups based on cuticle characters consisted of species of one genus only. This outcome did lend some support for the monophyly of the genera of the *Persea* group, but further research in the monophyly of these genera is hampered by a lack of specimens and the absence of revisions of the genera.

Alseodaphnopsis

Li et al. (2011) conducted the most extensive phylogenetic analysis of the *Persea* group to date. The genera *Machilus*, *Persea* and *Phoebe* were relatively well represented in their study, but *Alseodaphne*, *Dehaasia* and *Nothaphoebe* were very poorly represented (nine species of which two undescribed attributed to *Alseodaphne*, five species of which two unidentified attributed to *Dehaasia* and one species attributed to *Nothaphoebe*). They found that *Alseodaphne* fell into two clades, one including a few species of *Alseodaphe* (one of them the type species) and the *Dehaasia* and *Nothaphoebe* species, the other one comprising a few species of *Alseodaphne*. Recently Mo et al. (2017) analysed the *Alseodaphne* group again and confirmed that *Alseodaphne* was not monophyletic. Based on molecular and some morphological evidence they described the new genus *Alseodaphnopsis* H.W.Li & J.Li and included nine species (eight previously placed in *Alseodaphne* and one newly described) from southern China and adjacent India, Myanmar, Thailand, Laos and Vietnam in their new genus. Mo et al. (2017) did not find morphological characters in flowers or fruits that clearly separate *Alseodaphnopsis* from *Alseodaphne*. In the diagnosis of *Alseodaphnopsis* Mo et al. (2017) listed several characters in which *Alseodaphnopsis* was said to differ from *Alseodaphne* s.str. (Table 1).

Mo et al. (2017) presented two tables with measurements of fruits and inflorescences of a number of *Alseodaphne* species and most species of *Alseodaphnopsis*. They did not present data on the diameter or colour of the twigs, whether terminal buds are perulate or not, whether tepals are persistent or early deciduous, diameter of the petioles, leaf texture and whether midrib is sunken, flat or raised on the upper leaf surface. The lack of data makes it difficult to determine if any of the characters listed in Table 1 are diagnostic for *Alseodaphnopsis* or are simply more frequent among *Alseodaphnopsis* species than among *Alseodaphne* species. All diagnostic characters should be present in all species of *Alseodaphnopsis* and lacking in *Alseodaphne* s.str. Therefore the morphological basis for recognizing *Alseodaphnopsis* is unconvincing. Yet, molecular studies have shown that *Alseodaphne* is not monophyletic and it is to be expected that diagnostic morphological differences exist if the two clades of *Alseodaphne* represent two genera. Many species of *Alseodaphne* s.lat. are poorly known. Of the ten species of *Alseodaphne* s.lat. included in the Flora of China (Li et al. 2008), flowers were not known of four species; Kostermans (1973) described 14 new species known from one or two collections. This lack of good collections makes the finding of morphological diagnostic characters for *Alseodaphnopsis* difficult. Prior to the description of *Alseodaphnopsis* all Asian genera of the *Persea* group were defined by reproductive characters that were diagnostic.

Flowers of Alseodaphnopsis

All genera of the *Persea* group share a common flower structure. The flowers have two whorls of three tepals each; in most cases the six tepals are equal, but occasionally unequal with the outer three shorter than the inner three. Stamens are arranged in three whorls of three stamens each; stamens of the third whorl have each two glands at the base of the filaments. A fourth, innermost whorl is usually present and staminodial, but may be lacking entirely. The pistil is superior.

Alseodaphnopsis andersonii (King ex Hook.f.) H.W.Li & J.Li is a relatively common species of which several flowering collections are known. As part of a search for reproductive characters diagnostic for *Alseodaphnopsis* these flowering specimens were studied and two flower types were found to be present. One flower type has a large pistil and small stamens, the stamens shorter that the pistil and with anthers that show four locelli that do not open (Fig. 1a). The second type has a small pistil, shorter than the stamens and large stamens with open locelli (Fig. 1b). These different flower types can be explained in two ways. It could be that the flowers are unisexual and the species dioecious. But dioecy has never been reported for any member of the *Persea* group. In Asia, unisexual flowers in *Lauraceae* are only known in the *Litsea* group, a group of genera with flowers in umbels or pseudo-umbels. It is also possible that the two flower types are an example of dichogamy, a system in which

Table 1 Differences between *Alseodaphne* s.str. and *Alseodaphnopsis,* after Mo et al. (2017). Characters in **bold** are listed in the diagnosis of *Alseodaphnopsis* in Mo et al. (2017).

	Alseodaphne s.str.	*Alseodaphnopsis*
Twigs	2.5–4.5 mm diam, obviously whitish	4–11 mm diam, not obviously whitish
Terminal buds	Not or rarely perulate	Usually perulate, rarely not perulate
Tepals	Deciduous in young fruit	± Persistent at least in young fruit
Inflorescence size	3–20 cm long, 1–2 orders of branching, few-flowered	8.5–35 cm long, 3–4 orders of branching, many-flowered
Fruit size	0.7–3.5 cm, some with ribs	(1.3–)3–5 cm, without ribs
Petiole	1–1.5 mm diam	2–4 mm diam
Leaf texture	Variable (thinly chartaceous, chartaceous, thinly coriaceous or coriaceous)	Usually coriaceous, rarely chartaceous
Midrib upper surface	Raised or sunken	Usually sunken, sometimes flat

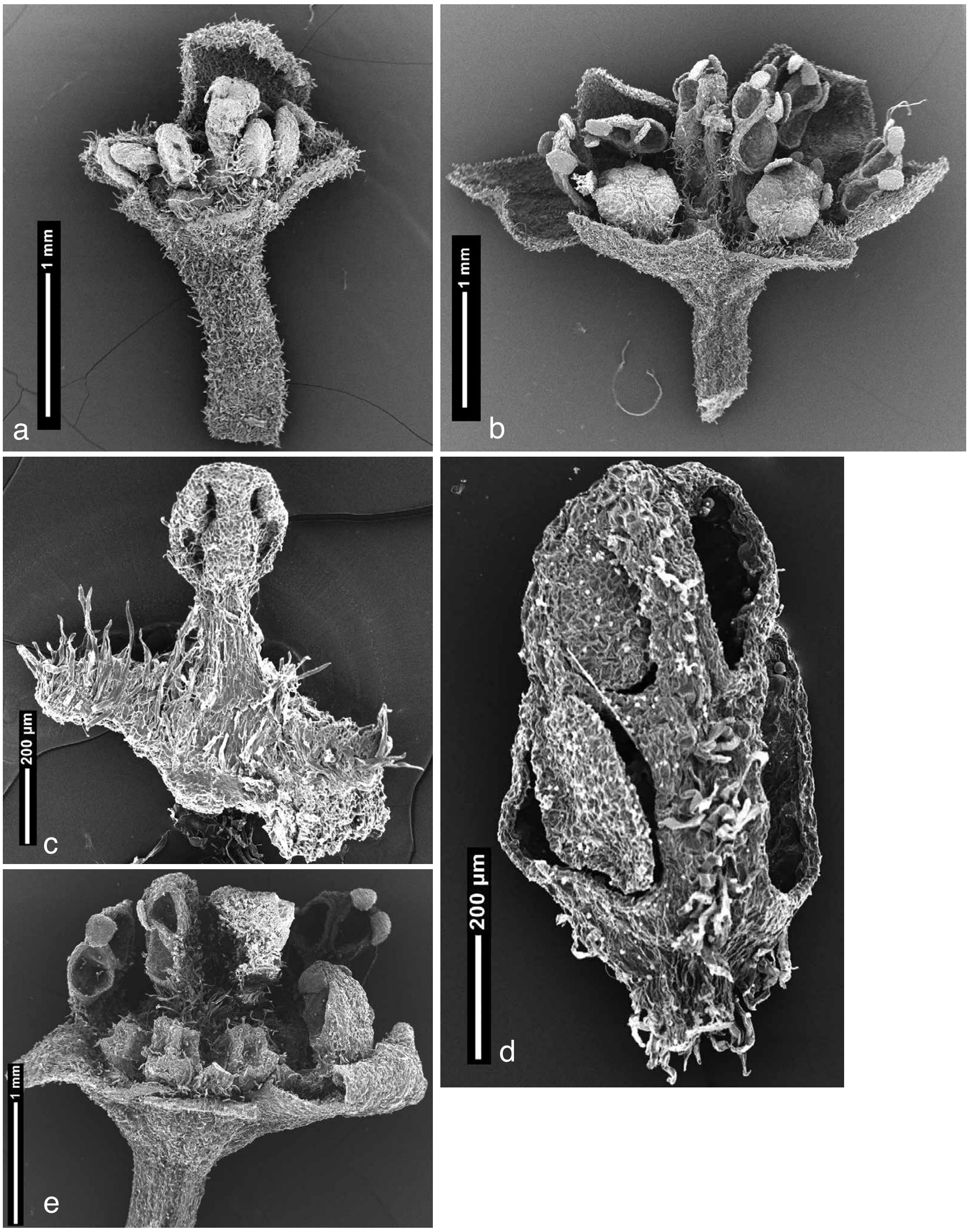

Fig. 1 a–d. *Alseodaphnopsis andersonii* (King ex Hook.f.) H.W.Li & J.Li. a. Pistillate flower. Several tepals removed. Note the large pistil and staminodes with rudimentary locelli; b. staminate flower. Two tepals removed. Note the slender, short pistillode and large stamens with opened locelli; c. staminode taken from the base of a young fruit; d. anther with small part of the filament. Note the large locelli, two with flaps still attached, two without the flaps. – e. *Alseodaphnopsis petiolaris* (Meisn.) H.W.Li & J.Li. Staminate flower. Several tepals removed. Note three of the outer six stamens and two stamens of the inner whorl. A pistillode is lacking. The three low bodies in the foreground are glands present at the base of the inner stamens (a. *Hyland 14931*, MO; b, d. *Poilane 30298*, P; c. *Van der Werff 23885*, MO; e. *Jitlan 12*, L).

the flowers pass through separate pistillate and staminate phases. During the pistillate phase the stamens are relatively undeveloped and the locelli remain closed, while the pistil is functional with a receptive stigma. During the following staminate phase the stamens develop further, the locelli open and shed pollen, while the stigma dries out and the pistil cannot be fertilized. Dichogamy was first demonstrated in the cultivated *Persea americana* Mill. (Stout 1927). Kubitzki & Kurz (1984) reported dichogamy for *Lauraceae* in Amazonian Brazil and I have observed dichogamy in species of *Licaria* Aubl. and *Cryptocarya*. Dichogamy thus appears to be a common flowering process among *Lauraceae* with bisexual flowers. Whether flowers are unisexual or bisexual with dichogamy can be determined most easily by examining the base of young fruits with remnants of floral parts. In the case of unisexual flowers, staminodes can be expected among floral remnants on young fruits; in the case of bisexual flowers stamens with opened locelli can be expected. In the case of *Alseodaphnopsis andersonii* staminodes were found at the base of young fruits (Fig. 1c). For comparison, Fig. 1d shows a stamen of *A. andersonii*. This confirms that the flowers of *Alseodaphnopsis andersonii* are unisexual. This is the first time that unisexual flowers have been found on any species of the *Persea* group. *Alseodaphnopsis lanuginosa* (Kosterm.) H.W.Li & J.Li was also found to have two flower types, similar to *Alseodaphnopsis andersonii* (pistillate flowers: *Pételot 3386bis*, MO; staminate flowers: *Pételot 3565*, MO). A single flowering collection of *Alseodaphnopsis petiolaris* (Meisn.) H.W.Li & J.Li (Fig. 1e) was found to have staminate flowers and an unidentified collection from Thailand (*Maxwell 07-702*, MO) has pistillate flowers. Because the type species of *Alseodaphnopsis*, *A. petiolaris*, was found to have unisexual flowers, I propose to accept as diagnostic character for *Alseodaphnopsis* the presence of unisexual flowers instead of the characters proposed by Mo et al. (2017). I would further accept in *Alseodaphnopsis A. andersonii*, *A. lanuginosa* and the unidentified species represented by *Maxwell 07-702*. These four species form a homogeneous group characterized by large, chartaceous leaves (mostly 20–30 cm long) and large inflorescences (20–30 cm long; *Maxwell 07-702* has inflorescences to 15 cm long). Two other species placed in *Alseodaphnopsis* by Mo et al. (2017), *A. hainanensis* (Merr.) H.W.Li & J.Li and *A. rugosa* (Merr. & Chun) H.W.Li & J.Li, appear quite different in their thick, coriaceous, narrowly elliptic to narrowly obovate leaves to 10 cm long. I have not seen flowers of these species. Their relationship is probably with *Alseodaphne rhododendropsis* Kosterm., a species from Central Vietnam. The other species placed by Mo et al. (2017) in *Alseodaphnopsis* are not known to me. *Alseodaphnopsis petiolaris*, *A. andersonii* and *A. lanuginosa* resemble each other closely and have been confused. Two collections of *Alseodaphnopsis lanuginosa*, *Pételot 3386* and *3386bis* (both at MO) were annotated by Kostermans as *Alseodaphne andersonii* and cited as such in the synopsis of *Alseodaphne* (Kostermans 1973); duplicates of *Pételot 3565* in L and MO, the type of *A. lanuginosa*, have labels copied by Kostermans from the original label of the holotype in P and give as altitude 400 m instead of 1 500 m on the holotype; three collections of *A. andersonii* in P (*Poilane 20964*, *30298* and *15704*) were initially identified as *A. petiolaris*; *Poilane 18974* (L) was identified and cited in Kostermans (1973), as *A. lanuginosa*, but appears to be *A. andersonii*.

Alseodaphne, *Dehaasia* and *Nothaphoebe* have never been revised. A better understanding of the species is necessary for a better understanding of the generic boundaries. Because the current concepts of the genera are based on flower characters – *Alseodaphne* with bisexual flowers, equal tepals and 4-locular stamens, *Alseodaphnopsis* with unisexual flowers, *Dehaasia* with 2-locular stamens, and *Nothaphoebe* with bisexual flowers, unequal tepals and 4-locular stamens –, revisions should be based on flowering specimens. As Kochummen (1989) already commented, describing new species in *Alseodaphne* or *Dehaasia* based on fruiting specimens alone is unwise. Once the four genera mentioned above have been revised, it will become possible to determine if those genera are monophyletic.

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