BLUMEA 46 (2001) 125–140

AN ANNOTATED KEY TO THE GENERA OF LAURACEAE IN THE FLORA MALESIANA REGION

HENK VAN DER WERFF

Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166, USA

SUMMARY

Lauraceae are an important component of wet tropical forests and are well represented in the Flora Malesiana region. Their identification has been hampered by two factors: several of the genera are poorly defined and existing keys require both flowers and fruits, which are, however, rarely present together on a specimen. Here a key based almost entirely on flowering specimens is presented, problems in generic delimitation are discussed and vegetative characters helpful in generic identification are listed.

Key words: Lauraceae, genera, key, Malesia, flowers, vegetative characters.

INTRODUCTION

Lauraceae are often an important component of wet, tropical forests and forests in the Flora Malesiana region form no exception. Many species are locally used for their wood or are commercially exploited. Still, for a variety of reasons, identification of Lauraceae to genus or species remains very difficult. Existing keys frequently require both flowers and fruits and because fruits of Lauraceae need several months before reaching maturity, both flowers and fruits are rarely present on herbarium specimens. Therefore, keys requiring flowers and fruits are essentially worthless for identification purposes.

Recently, some keys to genera of Lauraceae have been published for small parts of the FM area (Kochummen, 1989; Middleton, 2000). These keys do not include all genera found in the FM area and might not work outside the areas for which they were written. I thought it would be useful to present a key based on flowering material for all genera found in the FM area. Because of the small size of the flowers of Lauraceae, a good dissecting microscope is a necessary tool for identification. I recommend boiling up a few flowers when counting the number of stamens and anther locules. I also list several fruit and vegetative characters which seem helpful indicators for generic identification. Although I have seen many species in the smaller genera, I have not surveyed the large genera *Cryptocarya* R.Br. and *Litsea* Lam. and the full range of variation in vegetative characters in these genera is probably not expressed in the list of fruit and vegetative characters.

The brief descriptions given for each genus apply only to the species occurring in the FM area. Especially the larger genera may be more variable than the descriptions suggest; for example species of *Persea* Mill. and *Caryodaphnopsis* Airy Shaw may

have 2-locular stamens or 6 instead of 9 fertile stamens and a few Chinese species placed in *Litsea* have clustered leaves.

Sterile, fruiting or pistillate specimens cannot be identified with the key presented below. In some cases vegetative or fruit characters can help in identification of such specimens, while in other cases one has to recognize the specimen to species, because the generic characters are not visible.

CHARACTERS

Flowers

For a better understanding of the key and discussions I will briefly describe the flower structure of Lauraceae. Flowers of Lauraceae are either bisexual or unisexual. All species with unisexual flowers are dioecious. In unisexual flowers remnants of the other sex are usually present. In staminate flowers one may find a pistillode with a small stigma, a stipitiform pistillode without a stigma or a pistillode may be absent; in pistillate flowers the staminodia may have a remnant of an anther in the shape of a broadened tip, they may be threadlike without a trace of an anther or they may be absent. The degree of reduction of pistillode and staminodes is not well documented and is worth investigating.

In most, but not all, genera flowers are trimerous, with the whorls of floral parts in threes. From the outside towards the center one encounters the following whorls of floral parts: Tepals: arranged in two whorls, which are usually equal in shape and size, although sometimes they are unequal. In that case the inner whorl is as a rule larger than the outer whorl; the reverse, the outer whorl larger than the inner whorl, is very rare (*Triadodaphne* Kosterm.). Stamens: arranged in four whorls (I, II, III, IV, counted from the outside towards the inside) and opposite the tepals. Thus, stamens of whorl I are opposite the outer tepals, whorl II opposite the inner tepals, whorl III again opposite the outer tepals and whorl IV opposite the inner tepals. Stamens of whorl I and II appear to form one whorl of six. In most genera the stamens of whorl III bear at their base 2 globose glands; in a few cases the glands become enlarged and may form a cushion surrounding the stamens of whorl III (as in some species of *Endiandra* R.Br.) or enclosing all stamens (as in most species of the neotropical *Pleurothyrium* Nees). Reports of all stamens (if more than three) having glands at their base are mostly due to a misinterpretation of the greatly enlarged glands of whorl III enclosing all stamens. In *Cinnadenia* Kosterm. most or all stamens have glands at their base, but these glands are small in size and difficult to see, not surprising given the number of stamens and glands that are fitted in a small lauraceous flower. The stamens produce the pollen in small chambers, which open with flaps so characteristic for Lauraceae. The anthers have typically 4 or 2 locules; rarely do anthers have only 1 locule. The anther locules are either on the side of the anther facing the center of the flower (introrse) or facing towards the outside of the flower (extrorse). In most genera the stamens of whorl I and II have introrse locules, while whorl III is extrorse; in others all stamens are said to have introrse locules. The latter is the case in genera with umbellate inflorescences, in which the stamens have long filaments and the anthers are exserted. Because in these genera the filaments are long and often twisted, it is difficult to ascertain if the locules are all introrse or not and I have not

used this character in the key. In some cases (in *Endiandra*, for instance) the locules are lateral. In most species all stamens have the same number of locules; if this is not the case, stamens of whorl III tend to have fewer locules than those of whorl I and II. Flowers with 12 fertile stamens (whorls I, II, III, IV all fertile) usually have long filaments, so the anthers are exserted from the flower. When the stamens are shorter and included in the flower, there is not enough space for 12 fertile stamens and one or more whorls of stamens are reduced to staminodia. The first whorl to disappear is whorl IV, the innermost whorl; in some genera it is staminodial, in others it has completely disappeared. Sometimes additional whorls disappear and then flowers have only 6 or 3 fertile stamens. If only 3 stamens are present, these represent whorl III (*Endiandra, Eusideroxylon* Teijsm. & Binn. and *Triadodaphne*). An example of this trend towards reduction of number of stamens in smaller flowers is found in the genera *Potoxylon* Kosterm. and *Eusideroxylon*. By all accounts these genera are closely related; *Potoxylon* has larger flowers and 9 fertile stamens, while *Eusideroxylon* has much smaller flowers with 3 fertile stamens. The ovary is unicarpellate, unilocular and with one ovule. With few exceptions the ovary is superior and the fruit is seated unprotected on the pedicel, sometimes with persistent tepals at its base, or is seated in a cupule which can be shallow, plate-like or cup-shaped. In *Eusideroxylon* and *Potoxylon* the ovary is partially embedded in the receptacle and thus hemi-inferior; fruits in these genera are completely enclosed in and fused with the receptacle. *Cryptocarya* occupies an intermediate position; in flowers of this genus the ovary is enclosed in the receptacular tube, but not fused with it and thus technically superior; the fruits however are enclosed in and fused with the receptacular tube and are thus inferior.

Inflorescence types

The inflorescences of the Lauraceae (excluding *Cassytha* L.) can be divided into three main types (Van der Werff & Richter, 1996). Not all inflorescences can be assigned to one of these groups, because in some cases inflorescences have become strongly reduced while a few species or genera have inflorescences which simply do not match any of the three types.

In the first type the flowers are arranged in umbels, which, when young, are enclosed in decussate bracts. All flowers with this type of inflorescence are unisexual. The umbels can be single in the axils of leaves or bracts or they can be arranged along leafless shortshoots. Umbels can be sessile or stalked. When the umbels are arranged along a leafless shortshoot, the whole structure looks like a raceme of umbels, but in contrast to a raceme, the shortshoot has a vegetative terminal bud, which, after flowering, can grow into a normal leafy twig. Young umbels, still covered by the decussate bracts, can be easily mistaken for flower buds. However, the bracts surrounding the umbels are in pairs, whereas the tepals are in whorls of three.

In *Iteadaphne* Blume the umbels are reduced to a single flower; the presence of bracts at the base of the flower indicates that in this case the inflorescence consists of 1-flowered umbels and not of single flowers.

Inflorescences of the second type are paniculate-cymose. These inflorescences are repeatedly branched, with the flowers ultimately arranged in dichasia. The lateral flowers of such a dichasium are always strictly opposite (Fig. 1). Sometimes the inflorescences are racemose through reduction of the lateral axes.

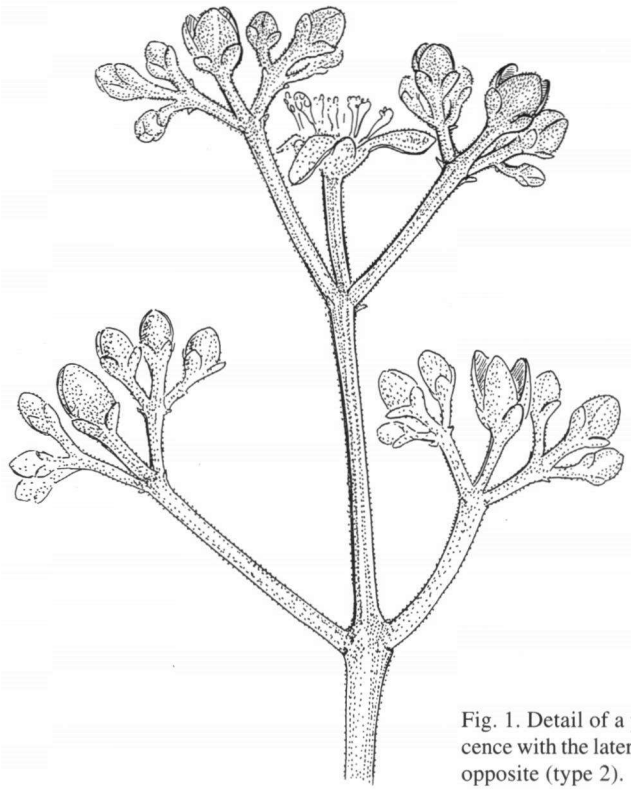

Fig. 1. Detail of a paniculate-racemose inflorescence with the lateral flowers of the cymes strictly opposite (type 2).

Inflorescences of the third type are also paniculate. However, the lateral flowers of the ultimate cymes are frequently not strictly opposite, and instead are somewhat alternate (Fig. 2). This is not always easy to see, especially not in species with very short pedicels and subsessile flowers (a condition not uncommon in *Cryptocarya*). Species of *Beilschmiedia* Nees and *Endiandra* tend to have longer pedicels which makes it easier to recognize this inflorescence type. *Potoxylon* has a predominantly racemose inflorescence with rarely three or four flowers together on the basal lateral branches of the inflorescence. This inflorescence is derived by reduction of the lateral branches from the inflorescence of the third type.

Two genera (*Actinodaphne* Nees and *Cinnadenia*) occur in the Flora Malesiana area which have inflorescences unlike the three types described above. The type species of *Actinodaphne,* as well as several other species placed in that genus, has a paniculate inflorescence which is enclosed in bracts when very young. These bracts do not appear to be decussate, but are alternate. They fall off very early in the development of the inflorescence, but leave a cluster of scars at the very base of the inflorescence. Inflorescences in *A. pilosa* (Lour.) Merr. are to 10 cm long, in *A. malabarica* Balakr. only 1–2 cm long and finally there are several species placed in *Actinodaphne* with a sessile pseudo-umbellate inflorescence, this still with bract scars at the very base. The difference between the *Actinodaphne* species with a pseudo-umbellate inflorescence and

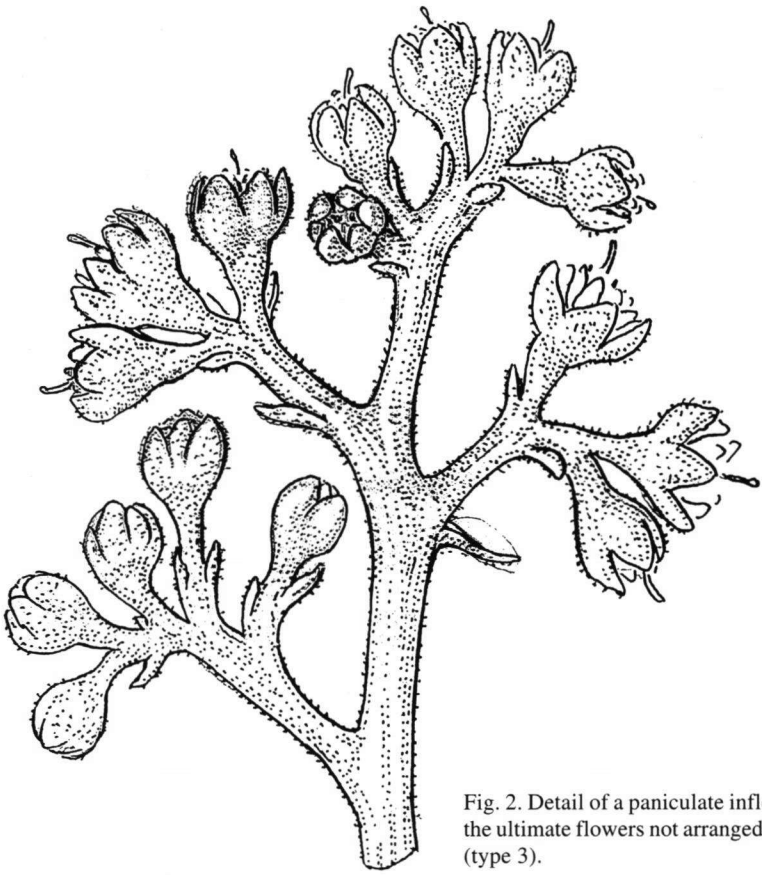

Fig. 2. Detail of a paniculate inflorescence with the ultimate flowers not arranged in strict cymes (type 3).

Litsea species with sessile umbels is difficult to see, especially in *Litsea* species with clustered leaves. Fortunately, the great majority (if not all) species of *Litsea* in the FM area have alternate or subopposite leaves, while *Actinodaphne* species generally have whorled leaves. The inflorescences of *Cinnadenia* are paniculate or racemose. If paniculate, the flowers (unisexual) are racemosely arranged along the secondary axes of the inflorescences.

Fruit and vegetative characters

Although floral characters are of prime importance for the determination of genera, fruit and vegetative characters can at times also be very helpful. One should keep in mind though that these characters only give an indication of generic assignment and that there may be many exceptions to these indications. Still, it is worthwhile to list some of these fruit and vegetative characters.

I have used the term perulate buds for vegetative buds covered by bracts. These bracts usually fall off after the buds elongate and leave distinct clusters of scars on the twigs. Only rarely (in some *Neolitsea* species) do the bracts persist as a short sheath at the base of the internodes.

In triveined leaves the main lateral veins depart from the midrib at the very base of the lamina, while in tripliveined leaves these veins leave the midrib a little above the base of the lamina.

- Fruits enclosed in the floral tube and with the scars of the fallen tepals on top of the fruit: *Cryptocarya, Eusideroxylon* and *Potoxylon*. *Eusideroxylon* and *Potoxylon* have large, rather slender fruits (more than 5 cm long, 2–3 cm wide) whereas *Cryptocarya* has fruits generally less than 5 cm long.
- Fruits seated in a cupshaped or bowlshaped cupule: *Litsea, Neolitsea* Merr. and *Actinodaphne*.
- Fruits with persistent, spreading to reflexed tepals at the base: *Persea*.
- Fruits with persistent, appressed tepals at the base: *Phoebe* Nees.
- Fruits seated unprotected on the pedicel, without persistent tepals or a cupule: *Alseodaphne* Nees, *Beilschmiedia, Brassiodendron* C.K. Allen, *Dehaasia* Blume, *Endiandra*.
- Twigs with pale, whitish bark, this contrasting with the dark petioles: *Alseodaphne, Dehaasia*.
- Leaves clustered, without perulate buds or clusters of scars along the branches: *Alseodaphne, Dehaasia, Phoebe*.
- Leaves clustered, with perulate buds and clusters of scars along the branches: *Actinodaphne, Neolitsea, Persea*.
- Leaves opposite: *Caryodaphnopsis, Cinnamomum* Schaeff. p.p., *Iteadaphne* Blume, *Litsea* p.p.
- Leaves triveined or tripliveined and opposite: *Caryodaphnopsis, Cinnamomum*.
- Leaves triveined, alternate: *Lindera* Thunb. p.p., *Neocinnamomum* H. Liu.
- Leaves tripliveined, alternate: *Cryptocarya* p.p., *Lindera* p.p.
- Terminal buds perulate: *Actinodaphne, Lindera* p.p., *Litsea* p.p., *Neolitsea, Persea*.
- Lower leaf surface glaucous: *Actinodaphne* p.p., *Alseodaphne* p.p., *Caryodaphnopsis, Cryptocarya* p.p., *Dehaasia* p.p., *Litsea* p.p., *Neolitsea* p.p.

PROBLEMS IN STUDYING LAURACEAE

When working with Lauraceae, two problems soon become apparent and I want to comment briefly on those:

1. A scarcity of good, flowering collections. No doubt this is due to the fact that many Lauraceae grow into rather tall trees and have small, inconspicuous flowers. Even though Lauraceae are often among the ten most common families in forest plots, good collections are few. This is reflected in nearly all revisions or floristic treatments (for instance Kostermans, 1986, in which most species treated are known from fewer than 10 collections). A welcome exception is the Revision of Lauraceae in Australia (Hyland, 1989) in which more than 20 collections were studied of the great majority of species. It took a team of dedicated field collectors several years to bring these collections together. For the FM area, good flowering collections are very much needed.
2. The poor delimitation of genera. In earlier classifications (reviewed in Van der Werff & Richter, 1996) generic delimitation was largely based on a numerical system: number of fertile stamens, number of anther locules, combined with inflores-

cence type, flowers (unisexual or bisexual), and fruit type. A classification based on these characters results in recognizable genera and allows the ordening of species in recognizable groups. As such, it is practical. Some genera, however, can be recognized by other characters than those listed above. An example is *Caryodaphnopsis*, with its opposite leaves, strongly unequal tepals and distinct wood anatomy. Species of that genus mostly have 9 4-locular stamens, but sometimes 9 2-locular stamens or even 6 2-locular stamens. This and other examples (see Van der Werff & Richter, 1996) indicate that androecial characters vary within monophyletic genera and their use in generic delimitation will likely result in the recognition of poly- or paraphyletic genera. Those who require that genera are monophyletic will likely have different generic circumscriptions than those who want a practical way of forming groups of species. One of the main aims of forming monophyletic groups is to express relationships between taxa. Because species of Lauraceae are still so incompletely known, it seems premature to try to develop a classification based on relationships and I have therefore tried to make a practical key towards the recognition of genera without taking into account if the genera are monophyletic. Ultimately I would prefer to recognize monophyletic genera and a classification reflecting the relationships between these genera, but the information needed for this is not yet at hand.

In two cases I was unable to recognize two generally accepted genera on floral characters. One case is *Persea* and *Phoebe*; because the fruit character used in earlier publications (for instance Kochummen, 1989) allows separation of the two, I include them both in my key. In the other case, *Alseodaphne* and *Nothaphoebe*, I did not find differences in flower or fruit between the two and have therefore included *Nothaphoebe* in *Alseodaphne*. Vegetatively, *Dehaasia* is very similar to *Alseodaphne* s.l. and, with the only difference between the two in the number of anther cells, description of new species in *Alseodaphne*, *Dehaasia* or *Nothaphoebe* based on fruiting collections has not helped our understanding of this group, as was pointed out by Kochummen (1989). More and better collections are needed to solve these problems.

KEY TO THE GENERA OF LAURACEAE IN THE FLORA MALESIANA AREA

1a. Herbaceous parasitic vine with leaves reduced to minute bracts .. **6. Cassytha**
b. Erect woody plants with regular leaves 2
2a. Flowers unisexual, arranged in umbels, these single in the axils of leaves or bracts, sometimes along leafless shortshoots or rarely (in some *Actinodaphne* species and *Cinnadenia*) paniculate 3
b. Flowers bisexual, inflorescences paniculate, rarely racemose 8
3a. Flowers dimerous 4
b. Flowers trimerous 5
4a. Inflorescences umbellate; terminal buds perulate; stamens 6 .... **18. Neolitsea**
b. Inflorescences paniculate; terminal buds not surrounded by bracts; stamens 18–32 ..... **7. Cinnadenia**
5a. Leaves whorled ..... **1. Actinodaphne**
b. Leaves alternate, rarely subopposite or opposite 6

6a. Anthers 4-locular ..... **16. Litsea**
b. Anthers 2-locular 7
7a. Umbels 1-flowered; leaves subopposite or alternate ..... **14. Iteadaphne**
b. Umbels with several flowers; leaves alternate ..... **15. Lindera**
8a. Anthers 2-locular 9
b. Anthers 4-locular 17
9a. Fertile stamens 3 10
b. Fertile stamens 6 or 9 11
10a. Tepals equal or the outer three slightly smaller than the inner three ..... **11. Endiandra**
b. Tepals unequal, the outer three much larger and covering the inner three, thus flowers apparently with only three tepals ..... **22. Triadodaphne**
11a. Fertile stamens 6 12
b. Fertile stamens 9 13
12a. Tepals longer than stamens, stamens included in the flower; anther cells lateral, slit-like ..... **4. Brassiodendron**
b. Tepals shorter than stamens, stamens exserted; anther cells extrorse, small, roundish ..... **13. Hexapora**
13a. Leaves opposite or subopposite ..... **8. Cinnamomum**
b. Leaves alternate or clustered 14
14a. Outer tepals clearly smaller (about half the size) than the inner ones ..... **10. Dehaasia**
b. Tepals equal or nearly so 15
15a. Flowers with a deep, tubular receptacle, this enclosing the ovary and later the fruit ..... **9. Cryptocarya**
b. Flowers with a shallow receptacle, the fruit unprotected on the pedicel or infrequently with small, persistent tepals at the base 16
16a. Lateral flowers of the ultimate cymes strictly opposite; bark of the twigs usually light-colored and contrasting with the much darker petioles ... **10. Dehaasia**
b. Lateral flowers of the ultimate cymes usually subopposite; twigs and petioles about the same color ..... **3. Beilschmiedia**
17a. Fertile stamens 3 ..... **12. Eusideroxylon**
b. Fertile stamens 9 18
18a. Leaves opposite, tri- or tripliveined 19
b. Leaves alternate, pinnately or triveined 20
19a. Tepals equal ..... **8. Cinnamomum**
b. Tepals unequal, the outer tepals much less than half the inner ones ..... **5. Caryodaphnopsis**
20a. Leaves triveined ..... **17. Neocinnamomum**
b. Leaves pinnately veined 21
21a. Inflorescences racemose or nearly so ..... **21. Potoxylon**
b. Inflorescences paniculate 22
22a. Tepals unequal, the outer ones about half as long as the inner ones ..... **2. Alseodaphne**
b. Tepals equal or nearly so 23

23a. Tepals deciduous or persisting as small scales at the base of the fruit ..... **2. Alseodaphne**
b. Tepals persisting in fruiting stage, conspicuous 24
24a. Tepals clasping the base of the fruit ..... **20. Phoebe**
b. Tepals spreading to reflexed in fruit ..... **19. Persea**

1. Actinodaphne Nees

Inflorescences paniculate or umbellate with clusters of bract scars at the very base. Flowers trimerous, unisexual, stamens 9, each with 4 locules, tepals equal. Fruit seated on a small, flat cupule. Leaves whorled, usually pinnately veined, sometimes glaucous below. Terminal buds usually perulate; clusters of scars present on the older twigs immediately above the whorls of leaves. Best recognized by its usually rather large, whorled leaves, and perulate terminal buds. Some species of *Litsea* may also have whorled leaves, but differ from *Actinodaphne* species with umbellate inflorescences in having the umbels generally stalked and in the absence of bract scars at the base of the inflorescence. About 100 species, tropical Asia with a few species in southern China.

2. Alseodaphne Nees (including *Nothaphoebe*)

Inflorescences of type 2. Flowers trimerous, bisexual, stamens 9, each with 4 locules, tepals unequal to equal. Fruit seated unprotected on the pedicel, this sometimes swollen and brightly colored, or small tepals persisting at the base of the fruit; a plate-like cupule rarely present (*A. insignis* Gamble). Leaves clustered near the tips of the twigs, pinnately veined, in several species glaucous below. Twigs often with conspicuous, light-colored bark, this contrasting with the darker petioles. Terminal buds not perulate. About 90 species, tropical Asia.

Various authors have tried to separate *Nothaphoebe* from *Alseodaphne*. Characters used for this include staminodia of whorl IV conspicuous, cordate-sagittate vs. staminodia much smaller, at most club-shaped; tepals unequal vs. tepals equal; fruiting pedicels thick, fleshy vs. fruiting pedicels cylindrical, not fleshy and tepals deciduous in fruit vs. tepals persistent in fruit. Of these characters, only tepals persistent vs. deciduous in fruit is a qualitative difference; the other ones are quantitative (tepals equal vs. unequal looks qualitative, but several species have subequal tepals and the distinction becomes therefore rather vague).

Bentham (1880) and Kostermans (1957) treated *Alseodaphne* and *Nothaphoebe* as sections or subgenera of *Persea*; Hutchinson (1964) included *Alseodaphne* in *Persea* and recognized *Nothaphoebe* as a distinct genus (however, in his key *Nothaphoebe* is included among the Tropical American genera). Kostermans (1973a) changed his opinion and recognized *Alseodaphne* and *Nothaphoebe* as valid genera. Even though Kostermans studied Asian Lauraceae more intensively than anybody else, he never developed a clear concept of *Alseodaphne* and *Nothaphoebe*. I found in BO two sheets of *Clemens 29777*; one was annotated in 1960 as the type of *Nothaphoebe clemensiae* Kosterm., the other was annotated in 1992 as the type of *Alseodaphne kinabaluensis* Kosterm. Neither of these names has been published, but these annotations underscore the difficulties of separating *Alseodaphne* and *Nothaphoebe*. It seems therefore best

to include *Nothaphoebe* in *Alseodaphne* although a study of all species involved is needed to determine if all should be placed in one or several genera. It is worth pointing out that several collections from the Neotropics are very similar to *Alseodaphne* s.l. and would certainly be described in *Alseodaphne* had they been collected in tropical Asia. Good flowering material of these species (apparently three undescribed species are involved) is needed for their description, but vegetative characters (thick twigs with pale bark, dark, long petioles, large, clustered leaves which are glaucous below) and thickened pedicels in fruit clearly point towards *Alseodaphne*.

3. Beilschmiedia Nees

Inflorescence paniculate (type 3). Flowers trimerous, bisexual, stamens 9, 2-locular; tepals equal, erect at anthesis, deciduous in older flowers. Fruit without a cupule, seated unprotected on the pedicel. Leaves alternate or subopposite, pinnately veined. I have not seen species with glaucous lower leaf surfaces. Terminal buds not perulate. About 250 species, pantropical.

This genus has been confused with *Dehaasia*, which has also bisexual flowers with 9 2-locular stamens. The best difference between the two is the inflorescence type; type 3 in *Beilschmiedia*, type 2 in *Dehaasia*. *Dehaasia* species have also frequently clustered leaves and twigs with pale bark and contrasting dark petioles. See also the note under *Endiandra*. A few Australian species placed in *Beilschmiedia* have persistent (but small) tepals at the base of the fruit; such species can be expected also in New Guinea. Whether these species are best included in *Beilschmiedia* or should be placed in a distinct genus, requires further study.

4. Brassiodendron C.K. Allen

Inflorescence paniculate (type 3), by reduction sometimes appearing racemose. Flowers trimerous, bisexual, stamens 6, 2-locular, tepals equal, half-erect or spreading at anthesis. Fruit without a cupule, seated unprotected on the pedicel. Leaves alternate, pinnately veined, lower leaf surface not glaucous. Terminal buds not perulate. 6 species, all from Australia with one species also in New Guinea.

These species do not form a homogeneous group and Hyland (1989) placed them in *Endiandra* and *Beilschmiedia*. Hyland's solution may well express their relationships better, but results in a key which is difficult to use and for practical reasons I recognize *Brassiodendron* as a distinct genus. The sole species occurring in New Guinea is closely related to *Endiandra*.

5. Caryodaphnopsis Airy Shaw

Inflorescence paniculate-cymose (type 2). Flowers trimerous, bisexual, stamens 9, 4-locular; tepals unequal, the outer 3 about 1/5 as long as the inner 3. Fruit without a cupule, unprotected on the pedicel. Leaves opposite, tri- or tripliveined, more or less glaucous below. Terminal buds not perulate. About 15 species in tropical Asia and tropical America, one species in the FM area (Philippines, Borneo, New Guinea).

Caryodaphnopsis is easily recognized by its opposite leaves and flowers with strongly unequal tepals. *Cinnamomum* species often have opposite, tripliveined leaves, but differ in having flowers with equal tepals.

6. Cassytha L.

Inflorescence a raceme. Flowers bisexual, trimerous, stamens 9, 2-locular; tepals unequal, the outer 3 much smaller than the inner 3. Fruit enclosed in the enlarged floral tube. Leaves alternate, minute, scale-like. Terminal buds not perulate. About 20 species, mostly in Australia, one species pantropical.

This herbaceous, parasitic vine cannot be confused with any other genus of Lauraceae; sometimes it is confused with *Cuscuta* (Convolvulaceae).

7. Cinnadenia Kosterm.

Inflorescence a panicle. Flowers unisexual, trimerous or dimerous (see discussion), tepals equal, number of stamens variable (9–32), 4-locular. Fruit seated on a small, plate-like cupule. Leaves alternate, pinnately veined. Terminal buds not perulate. A rarely collected genus of two species, one in Peninsular Malaysia.

The only other genus with unisexual flowers and a paniculate inflorescence is *Actinodaphne*, which differs in having whorled leaves, perulate terminal buds, and flowers with 9 stamens (18–32 in *C. malayana* Kosterm.). Kostermans (1973b) described the type species as having trimerous flowers, as did Long (1984). Kochummen (1989) mentioned that the flowers of *C. malayana* he had seen were dimerous, but Kostermans (1977) mentioned that the stamens are in whorls of 3, suggesting that the flowers are trimerous. I have seen an isotype of *Litsea liyuyingii* H. Liu, which Kostermans (1973b) treated as a synonym of *Cinnadenia paniculata* (Hook.f.) Kosterm., and this has dimerous flowers. *Cinnadenia* is a poorly known genus; I have not seen material of *C. malayana* and base my view of this species (and thus the concept of *Cinnadenia* in this article) on Kochummen's (1989) observations. Dr. J. Rohwer (pers. comm.) checked a flower of *C. malayana* and found it to have 4 tepals and 28 stamens which became progressively smaller towards the center of the flower.

8. Cinnamomum Schaeff.

Inflorescences paniculate-cymose (type 2). Flowers trimerous, bisexual, stamens 9, 4-locular; tepals equal, half-erect at anthesis. Fruit seated in a small cupule, this with or without persistent tepals or the tepals partly persistent. Leaves either opposite and tripliveined or alternate and pinnately veined; rarely leaves alternate and tripliveined. About 350 species, mostly in tropical and subtropical Asia, but also present in Australia, Oceania and tropical America.

Species with tripliveined leaves usually lack perulate buds, while species with pinnately veined leaves have perulate buds. A few species from the Philippines and Irian Jaya have 9 2-locular anthers (Kostermans, 1986) instead of 4-locular anthers. The opposite, tripliveined leaves combined with flowers with equal tepals allow easy identification of most *Cinnamomum* species in the FM area; one or two species have alternate, pinnately veined leaves and perulate terminal buds.

9. Cryptocarya R.Br.

Inflorescences paniculate (type 3). Flowers trimerous, bisexual, stamens 9, 2-locular; tepals equal, half-erect to spreading at anthesis. Fruit entirely enclosed in the enlarged

floral tube, at the tip with small scars from the fallen tepals, frequently with longitudinal ribs. Leaves alternate, pinnately or in a few species tripliveined. Terminal buds not perulate. Several species have somewhat oblong leaves, an uncommon leaf shape among Lauraceae, but this might also occur in *Litsea*. Glaucous lower leaf surfaces are not rare. A large genus of more than 300 species, pantropical, with the majority of species in tropical Asia.

The flowers with their 9 2-locular stamens and deep floral tube are distinctive. Two monotypic genera, *Eusideroxylon* and *Potoxylon*, have also fruits fully enclosed in enlarged floral tubes, but both have much larger (more than 5 cm long) fruits.

10. **Dehaasia** Blume

Inflorescences paniculate-cymose (type 2). Flowers trimerous, bisexual, stamens 9, 2-locular; tepals unequal (the outer 3 much smaller than the inner 3) to almost equal, deciduous or persistent, but not enlarged, in fruit. Fruit unprotected on the pedicel, sometimes with very small, persistent tepals at the base, the fruiting pedicel in some species swollen and colored. Leaves alternate, clustered near the tips of the branches, pinnately veined, sometimes glaucous below. In some species the twigs have a pale to whitish bark, which contrasts with the dark petioles (this is also the case in *Alseodaphne* species). Terminal buds not perulate. About 35 species, tropical Asia.

Dehaasia is closely related to *Alseodaphne*, from which it differs only in having 2-locular instead of 4-locular anthers. Vegetatively, it is indistinguishable from *Alseodaphne* and without stamens assigning a specimen to either of these genera is a guess.

11. **Endiandra** R.Br.

Inflorescences paniculate (type 3). Flowers trimerous, bisexual, stamens 3, 2-locular; tepals equal, rarely subequal (with the outer tepals slightly smaller than the inner ones), half-erect to spreading at anthesis. Fruit unprotected on the pedicel, the tepals deciduous in fruit. Leaves alternate, pinnately veined, not glaucous below. Terminal buds not perulate. In some species the glands at the base of the stamens become greatly enlarged and are united, forming a disc surrounding the stamens and pistil. About 100 species, tropical Asia, Australia and the Pacific.

In the FM area only two other genera have flowers with 3 fertile stamens: *Triadodaphne* which differs in having the outer tepals much larger than the inner ones, and *Eusideroxylon*, which has 4-locular stamens and large staminodia (representing whorl I and II). Vegetatively *Endiandra* is similar to *Beilschmiedia*, and fruiting specimens can often not be assigned to either genus with certainty.

12. **Eusideroxylon** Teijsm. & Binn.

Inflorescence laxly paniculate (type 3). Flowers trimerous, bisexual, stamens 3, 4-locular; staminodes representing whorl I and II well developed; tepals equal, more or less erect at anthesis. Fruit entirely enclosed in the accrescent floral tube, at the tip with small scars from fallen tepals. Leaves alternate, pinnately veined, not glaucous below. Terminal buds not perulate. Wood very hard. 1 species, Borneo and Sumatra.

Vegetatively very similar to *Potoxylon*, but differs in its laxly branched inflorescences and flowers with only three fertile stamens.

13. **Hexapora** Hook.f.

Inflorescence paniculate (type 3) or racemose. Flowers trimerous, bisexual; stamens 6, 2-locular; tepals equal, erect at anthesis, shorter than the stamens. Fruit with persistent tepals and stamens at the base (Kochummen, 1989). Leaves alternate or somewhat clustered, pinnately veined, not glaucous below. Terminal buds not perulate. A monotypic genus, rarely collected and only known from Penang, Peninsular Malaysia.

Hexapora is best recognized by its 6 2-locular stamens with round locules representing whorl I and II and by the extrorse locules, which is very unusual for stamens of whorl I and II. *Brassiodendron* has also 6 2-locular stamens, but these are lateral and have long, slit-like anther cells. Neither tepals nor stamens persist in fruit.

14. **Iteadaphne** Blume

Inflorescence umbellate, the umbels 1-flowered, a few together along a slender, leafless shortshoot. Flowers trimerous, unisexual; stamens 6–9, 2-locular, tepals equal or subequal. Fruit not seen, said to be seated on a small cupule. Leaves opposite or subopposite, pinnately veined, not glaucous below. Terminal buds not perulate. A monotypic genus from Java and Sumatra, closely related to *Lindera*, but differing in its 1-flowered umbels and wood anatomy (Richter, 1981).

I am not certain *Iteadaphne* deserves recognition on generic level. A species from S China and NE India has also been placed in *Iteadaphne* [*I. caudata* (Nees) H.W. Li]. This species has also 1-flowered umbels with 2-celled stamens along leafless shortshoots, but differs in having alternate, strongly tri- or tripliveined leaves. It is likely that the recently described *Lindera spicata* Kosterm. (Kostermans, 1992) is closely related to *I. caudata* and that the buds of *L. spicata* are young, bracteate inflorescences. I expect that a more thorough study will find that the reduction of multi-flowered umbels to 1-flowered umbels in *Lindera* has taken place more than once and that *I. confusa*, with its opposite or subopposite, pinnately veined leaves is not closely related to *I. caudata* and *L. spicata*, which have alternate, tri- or tripliveined leaves.

15. **Lindera** Thunb.

Inflorescence umbellate, umbels with several flowers, along a shortshoot or in axils of leaves. Flowers trimerous, unisexual; stamens 9 or more, 2-locular, tepals equal or nearly so. Fruit with or without a small cupule. Leaves alternate, pinnately or tripliveined, the lower surface sometimes glaucous. Terminal buds perulate or not. A genus of about 100 species, mostly in tropical and subtropical Asia with a few species in temperate N America; relatively few species in the FM area.

Lindera differs from *Litsea* only in its 2-locular (not 4-locular) anthers and fruiting specimens or specimens with pistillate flowers are difficult to determine to genus.

16. **Litsea** Lam.

Inflorescence umbellate, umbels with several flowers, along shortshoots or in axils of leaves. Flowers trimerous, unisexual; stamens usually 9, 4-locular, tepals equal or lacking. Fruit with a small to rather large cupule. Leaves alternate or rarely opposite,

pinnately veined, sometimes glaucous below. Terminal buds perulate or not. A large genus, more than 300 species, mostly in tropical Asia, also present in Oceania, Australia and in N and C America.

Litsea is characterized by its umbellate inflorescences, trimerous flowers and 4-locular anthers. It is a large genus in the FM area and one may expect a great deal of morphological variation in the genus. Although I have not seen species with clustered or tripliveined leaves in the FM area, I would not be surprised if they exist. The short-shoots bearing the inflorescences can be quite long (up to 10 cm, and making the term shortshoot illogical) in some species and the umbel-bearing shoot looks much like a raceme of umbels; however, there is always a vegetative terminal bud indicating the 'raceme' is a twig bearing umbels.

17. **Neocinnamomum** H. Liu

Inflorescence paniculate-cymose, the cymes often sessile and the flowers in fascicles or inflorescence reduced to a single fascicle. Flowers trimerous, bisexual; stamens 9, 4-locular, tepals equal, half-erect at anthesis. Fruit on an obconical, swollen pedicel, tepals persistent. Leaves alternate, strongly tri- or tripliveined, not glaucous below. Terminal buds not perulate. A genus of 6 species in tropical Asia, with 1 poorly known species from Sumatra.

The fascicled flowers, tri- or tripliveined, alternate leaves, and the swollen pedicel with persistent tepals in fruit make recognition rather easy.

18. **Neolitsea** Merr.

Inflorescence umbellate, umbels with several flowers, single or several close together along a shortshoot. Flowers dimerous, unisexual; stamens 6, 4-locular; tepals equal, 4, spreading at anthesis. Fruit seated on a small, plate-like cupule, the tepals sometimes initially persisting, but ultimately falling off. Leaves generally clustered, tripliveined and sometimes glaucous below. Terminal buds perulate. About 100 species, mostly in tropical Asia, but extending to Australia.

Neolitsea is best recognized by its dimerous flowers although in other characters it is close to *Litsea*. Some vegetative characters help separate the two genera: *Neolitsea* has usually clustered, tripliveined leaves and sessile umbels, these frequently borne along the leafless parts of the innovations, while *Litsea* has usually alternate (rarely opposite), pinnately veined leaves and stalked umbels, these usually in the axils of leaves or along shortshoots. Some *Litsea* species also have rather large, cup-shaped cupules. In a few species of *Neolitsea* the bracts surrounding the terminal buds persist as a sheath at the base of the leafless internodes.

19. **Persea** Mill.

Inflorescence paniculate-cymose (type 2). Flowers trimerous, bisexual; stamens 9, 4-locular; tepals equal or subequal, half-erect at anthesis. Tepals persistent at the base of the fruit, spreading to reflexed, a cupule absent. Leaves alternate or slightly clustered, pinnately veined, sometimes glaucous below. Terminal buds perulate. A poorly defined genus with c. 200 species in tropical Asia and America with a few species in subtropical regions of the Northern Hemisphere.

The description given above applies only to the Asian species, which are sometimes placed in the segregate genus *Machilus*. I have not found floral differences between Asian *Persea* species and *Phoebe* and these two groups are usually separated on fruit characters. In Asian *Persea* species the tepals are persistent and spreading to reflexed in fruit, in *Phoebe* they are persistent and pressed against the fruit. Difficulties with generic delimitation in this group are partly due to the great variation found in American species placed in *Persea*. Some of these have equal tepals deciduous in fruit (including the type species, *P. americana* Mill.), others have equal tepals persistent in fruit (but the tepals neither spreading nor pressed against the fruit as in *Phoebe*), or unequal tepals (the outer 3 much smaller than the inner 3) persistent in fruit while one species (*P. julianae* van der Werff from Surinam) has strongly unequal tepals which are deciduous in fruit. A comprehensive study of *Persea* s.l. and *Phoebe* is needed for the establishment of clear generic boundaries.

20. **Phoebe** Nees

Inflorescence paniculate-cymose (type 2). Flowers trimerous, bisexual; stamens 9, 4-locular; tepals equal or subequal, more or less erect at anthesis. Tepals persistent and clasping the base of the fruit, a cupule absent. Leaves alternate or slightly clustered, pinnately veined, sometimes glaucous below. Terminal buds usually not perulate. Tropical Asia, c. 100 species.

As discussed under *Persea*, *Phoebe* can be separated from *Persea* only by the clasping vs. spreading tepals in the fruiting stage. It is my impression that *Phoebe* is better represented in the FM area than *Persea*, that species with obovate leaves are quite common in *Phoebe* and that *Phoebe* species generally lack perulate buds.

21. **Potoxylon** Kosterm.

Inflorescence racemose or with a few flower clusters near the base of the inflorescence. Flowers trimerous, bisexual; stamens 9, 4-locular; tepals equal, more or less erect at anthesis. Fruit enclosed in and fused with the accrescent floral tube. Leaves alternate and pinnately veined, not glaucous below. Terminal buds not perulate. A monotypic genus known only from Borneo.

Potoxylon is vegetatively very similar to *Eusideroxylon*, but the flowers are much larger and with 9 fertile stamens and the inflorescence is basically racemose (laxly paniculate in *Eusideroxylon*).

22. **Triadodaphne** Kosterm.

Inflorescence paniculate (type 3). Flowers trimerous, bisexual; stamens 3, 2-locular; tepals strongly unequal, the outer 3 much larger and almost completely covering the inner 3, more or less erect at anthesis. Fruit not known. Leaves alternate and pinnately veined, not glaucous below. Terminal buds not perulate. A monotypic genus known only from Borneo.

Triadodaphne was included by Rohwer (1993) in *Endiandra*, but I prefer to recognize it based on its strongly unequal tepals with the outer 3 much larger than the inner 3 and the much deeper receptacle. Kostermans (1993) included 2 additional species

in *Triadodaphne*, *T. inaequitepala* (Kosterm.) Kosterm. from New Guinea and *T. pachytepala* Kosterm. from the Solomon Islands. The specimen I saw of *T. inaequitepala* had the outer tepals shorter than the inner ones (but not greatly so) and I would include that species in *Endiandra*, where it was initially placed. I have not seen material of *T. pachytepala*.

ACKNOWLEDGEMENTS

This article is based largely on observations made during a 4-week stay at BO and I would like to express my thanks to the Director and Staff members who did their very best to make my visit a pleasant and productive one. I also thank Peter Stevens for critically reading the manuscript. Figures 1 and 2 were previously published in the Annals of the Missouri Botanical Garden 83: 417 (1996).

REFERENCES

Bentham, G. 1880. Laurineae. In: G. Bentham & J.D. Hooker, Genera Plantarum 3, 1: 146–168. Lovell Reeve & Co., Williams & Norgate, London.

Hutchinson, J. 1964. The Genera of Flowering Plants (Dicotyledonae), vol. 1. Clarendon Press, Oxford.

Hyland, B.P.M. 1989. A revision of the Lauraceae in Australia (excluding Cassytha). Aust. Syst. Bot. 2: 135–367.

Kochummen, K.M. 1989. Lauraceae. In: F.S.P. Ng (ed.), Tree Flora of Malaya, vol. 4: 98–178. Longman, Malaysia.

Kostermans, A.J.G.H. 1957. Lauraceae. Comm. For. Res. Inst. 57: 1–64.

Kostermans, A.J.G.H. 1973a. A synopsis of Alseodaphne Nees (Lauraceae). Candollea 28: 93–136.

Kostermans, A.J.G.H. 1973b. Cinnadenia Kosterm. Genus Novum Lauracearum. Adansonia sér. 2, 13: 223–227.

Kostermans, A.J.G.H. 1977. Notes on Asian Lauraceae. Adansonia sér. 2, 17: 89–93.

Kostermans, A.J.G.H. 1986. A monograph of the genus Cinnamomum Schaeff. (Lauraceae), Part 1. Ginkgoana 6: 1–171.

Kostermans, A.J.G.H. 1992. Two remarkable Lindera species (Lauraceae) probably representing an undescribed genus. Reinwardtia 11: 23–26.

Kostermans, A.J.G.H. 1993. Notes on Triadodaphne Kosterm. (Lauraceae). Rheedia 3: 129–131.

Long, D.G. 1984. Lauraceae. In: A.J.C. Grierson & D.G. Long (eds.), Flora of Bhutan, vol. 1, part 2: 250–281. Royal Botanic Garden, Edinburgh.

Middleton, D.J. 2000. Lauraceae. In: G. Argent et al. (eds.), Manual of the larger and more important non dipterocarp trees of central Kalimantan, Indonesia. Forest Research Institute, Samarinda, Indonesia.

Richter, H.G. 1981. Anatomie des sekundären Xylems und der Rinde der Lauraceae. Sonderb. Naturw. Vereins Hamburg 5: 1–148.

Rohwer, J.G. 1993. Lauraceae. In: K. Kubitzki, J.G. Rohwer & V. Bittrich (eds.), The Families and Genera of Vascular Plants II: 366–391. Springer Verlag, Berlin.

Van der Werff, H. & H.G. Richter. 1996. Toward an improved classification of Lauraceae. Ann. Missouri Bot. Gard. 83: 409–418.