TOWARD AN IMPROVED CLASSIFICATION OF LAURACEAE[1]

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ABSTRACT

Published suprageneric classifications of Lauraceae and the characters used in these classifications are briefly reviewed. It is concluded that androecial characters such as number of stamens and number of anther cells are often variable even within genera and that these characters should not be used in a classification of Lauraceae. As a first step toward an improved classification, Lauraceae are divided into two subfamilies, one consisting of *Cassytha*, the other including all other genera. The latter group is divided into three tribes, the Laureae, Perseeae, and Cryptocaryeae, based on characters of wood and bark anatomy and inflorescence structure.

Lauraceae form a large, predominantly tropical family of trees and shrubs, with the exception of *Cassytha*, an herbaceous parasite. The family is best represented in the American and Asian tropics, and has also a rather large number of species in Australia and Madagascar, but is poorly represented in Africa. About 50 genera are currently recognized, with 2500–3000 species.

Economically, Lauraceae are an important group. Many species yield high-quality timber, others spices or aromatic oils, and *Persea americana* Miller is cultivated worldwide for its edible fruits.

Ecologically, Lauraceae are, in the New World, a very important group. They are present in wet forest at any elevation (from sea level to *páramos*) and are frequently the most common or one of the most common tree families, especially in the foothills and at middle elevations of the Andes.

In spite of their importance, Lauraceae are, in respect to classification and species numbers, poorly known. Our lack of knowledge of species numbers and distribution is no doubt related to the fact that many species are tall trees with small, inconspicuous flowers, difficult to locate and to collect. This is clearly shown by a recent floristic treatment (Australia: 115 species, of which 46 were new, Hyland, 1989), recent revisions (*Nectandra:* 114 species, of which 33 were new, Rohwer, 1993a; *Pleurothyrium:* 40 species, of which 20 were new, van der Werff, 1993), and the fact that in the most recent monograph of *Aniba* (Kubitzki, 1982) not a single collection was recorded from Ecuador, while currently 11 species are known from that country. More intensive collecting will hopefully correct this lack of knowledge.

Lauraceae have, with a few exceptions, trimerous flowers. Flowers are bisexual or unisexual. There are two whorls of three tepals; the whorls are usually equal in size and shape, but in some cases the whorls are unequal. If the whorls are unequal, the outer whorl is usually smaller than the inner one, although the reverse can also be the case. Flowers have four whorls of three stamens, but in most genera, one, two, or three whorls are reduced to staminodia. The anthers open by two or four valves. The ovary is generally superior, with one locule and one ovule, and the fruit, a one-seeded berry, sits either free on a pedicel, is partially enclosed by persistent tepals or the receptacle, or is entirely enclosed by the receptacle.

CLASSIFICATION OF LAURACEAE

Strictly speaking, there is no lack of suprageneric classifications of Lauraceae. All have in common one characteristic: they are not widely accepted. We will present a brief review of these classifications and list the main characters used in making them. The position of *Cassytha* in the different classifications will not be discussed; it is always separated from the other Lauraceae because of its herbaceous, parasitic habit, and we place it in its own subfamily, the Cassythoideae.

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Characters Used in
Nees (1836) Classification

1) Leaves deciduous vs. evergreen.
  2) Inflorescence umbellate or glomerate.
    a) Inflorescence umbellate, involucrate.
    b) Inflorescence glomerate or subracemose, arising from perulate buds.
  2) Inflorescence paniculate.
    3) Anthers opening apically.
    3) Anthers opening below tip, equal.
    3) Outer anthers petaloid.
    3) Anthers with distinct filaments.
      4) Fruits covered by perianth tube.
      4) Fruits not protected by perianth tube.
        5) Staminodia lacking or, if present, without capitate apex.
        5) Staminodia with triangular head.
          6) Tepals entirely persistent
            7) in a solid cup
            7) spreading, not thickened
          6) Tepals largely deciduous
            7) Truncate base,only, persistent.
            7) Entirely deciduous.

Figure 1. Main characters used in Nees's (1836) classification.

Meissner
1) Suborder Laurineae
2) Suborder Gyrocarpeae, excluded from Lauraceae
3) Suborder Cassytheae, *Cassytha*

Laurineae:

A. Inflorescence paniculate, racemose or spicate. No involucres.
  Tribus Perseaceae:
  Flowers hermaphrodite. Stamens 9. Cupule present or lacking. Staminodia well developed.
    1) 4-celled anthers; 6 genera
    2) 2-celled anthers; 6 genera
  Tribus Oreodophneae:
  Flowers unisexual, cupule present or lacking.
    a) Stamens free, 4-celled, inner 3 extrorse; 7 genera (*Ocotea* s.l., *Nectandra, Pleurothyrium*)
    b) Stamens free, 4-celled, all introrse; 2 genera (*Sassafras, Sassafridium*)
    c) Stamens free, 2-celled, inner 3 extrorse; 1 genus (*Goeppertia*)
    d) Stamens fused, flowers hermaphrodite; 2 genera (*Symphysodaphne, Synandrodaphne*)
  Tribus Cryptocaryeae:
  Flowers hermaphrodite, fruits enclosed in calyx.
    1) Flowers 4-merous. *Adenostemum*, excluded.
    2) Flowers 3-merous, 2-celled. 10 genera, including: *Cryptocarya, Aiouea, Ampelodaphne*
    3) Flowers 3-merous, capitate, 2-celled; stamina monadelphic. *Misantheca.*
    4) Flowers 3-merous, 4-celled, stamens free. 4 genera

B. Flowers umbellate or glomerulate. Involucrum present.
  Tribus Litseaceae:
    Subtribus Tetranthereae. Anthers 4-celled; 5 genera
    Subtribus Daphnidieae. Anthers 2-celled; 5 genera

Figure 2. Main characters used in Meissner's (1864) classification.

It has been suggested that *Cassytha* is closely related to *Cryptocarya* (Rohwer, 1993b); however, the main characters discussed in this paper (inflorescence structure and wood and bark anatomy) will not elucidate the relationsips of *Cassytha.* The classifications by Nees (1836; Fig. 1), Meissner (1864; Fig. 2), Bentham and Hooker (1880; Fig. 3), Pax (1889; Fig. 4), Mez (1889; Fig. 5), and Hutchinson (1964; Fig. 6) are all based on the following characters: inflorescence paniculate versus umbellate; number of anther cells (2 vs. 4); number of stamens; fruit enclosed in perianth versus seated in a cup or free; and flowers unisexual or bisexual. These classifications are strongly influenced by the choice of the most important character, and differences between the classifications are a result of such choices and are not based on new or better data. For instance, Pax used 2- versus 4-celled anthers as the most important character, while Mez and Nees used inflorescence paniculate versus racemose. None of these authors defends or explains his determination of the importance of the characters, and all classifications are in some aspects confusing. Several of these classifications include genera no longer recognized or which were based on faulty diagnoses, but such details are of historical interest only.

Kostermans (1957) published a new classification, in which he recognized five tribes (Fig. 7). One tribe was recognized by its involucrate inflorescence, the other four non-involucrate tribes by the development or lack of cupules. One tribe was recognized by a complete absence of a cupule (for example, *Persea* and *Beilschmiedia*), the second by the presence of a more or less cup-shaped cupule (*Ocotea, Nectandra*), the third by having the fruit almost completely enclosed by the cupule (*Cryptocarya,* for example), and the fourth by having a truly inferior ovary and the fruit entirely enclosed by the hypanthium (only *Hypodaphnis*). Further division within the tribes is primarily based on number of anther cells. In comparison with the contemporary classification of Hutchinson (1964), Kostermans's classification is clearly superior, not because the characters used for the classification are sounder, but because he knew the Lauraceae well. Thus, he excluded a number of weak genera recognized by Hutchinson, and avoided errors that Hutchinson, less experienced with Lauraceae, made. Kostermans's classification has found general acceptance during the last 30 years, although sev-

Bentham and Hooker (1880)

3 TRIBES

1) Perseaceae. Stamens of whorl III opening extrorse, with 2 basal glands, inflorescences lax, pedunculate.
   a) Anthers 2-celled. Fruit included in perianth.
   b) Anthers 2-celled. Fruit with / without cupule. subdivided by number of stamens.
   c) Anthers 4-celled.Fruit with/without cupule subdivided by number of stamens.

2) Litseaceae. Trees or shrubs. All stamens opening introrse. Inflorescence dense, short, subsessile (except Sassafridium).
   a) Inflorescence lax or imbricate - bracteate.
   b) Inflorescence umbellate or capitate, included in an involucre. Subdivided by number of anther cells.

3) Cassytheceae. Leafless vines.

Figure 3. Main characters in Bentham & Hooker's (1880) classification.

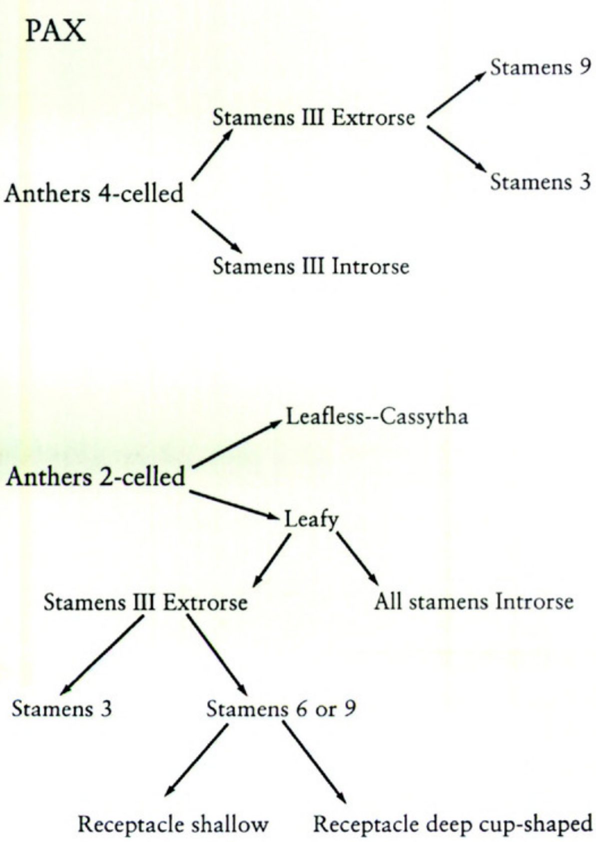

Figure 4. Main characters used in Pax's (1889) classification.

Mez

Herbaceous parasitic vine; inflorescence indeterminate .... ***Cassytheae***
Shrubs or trees, inflorescence determinate .... ***Laureae***
  Inflorescences paniculate, exinvolucrate ..... ***Perseeae***
    Anthers of outer two whorls 2-celled or sterile ....
    Anthers of outer two whorls 4-celled ....
  Inflorescences racemose, involucrate .... ***Litseeae***
    Anthers 2-celled ....
    Anthers 4-celled ....

Figure 5. Main characters used in Mez's (1889) classification.

eral workers have pointed out difficulties with generic circumscription and classification (Hyland, 1989; Rohwer et al., 1991; van der Werff, 1991). Richter (1981) published the results of his study of wood and bark anatomy of Lauraceae, in which he found three large groupings of genera (Fig. 8). One of the groups corresponds with the tribe including genera with involucrate inflorescences, but the other two groups have no counterpart in the existing classifications. For instance, Richter placed *Cryptocarya* and *Beilschmiedia* in the same group, while in Kostermans's classification they occupy very different positions.

The most recent classification is by Rohwer (1993b). He recognized two main groups, based on inflorescence type, one involucrate and one exinvolucrate. Further divisions were based on fruit and floral characters, but because these characters were

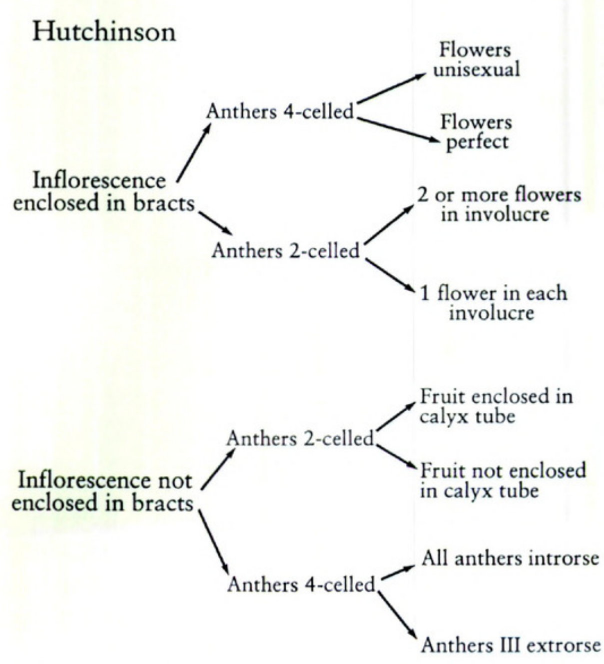

Figure 6. Main characters used in Hutchinson's (1964) classification.

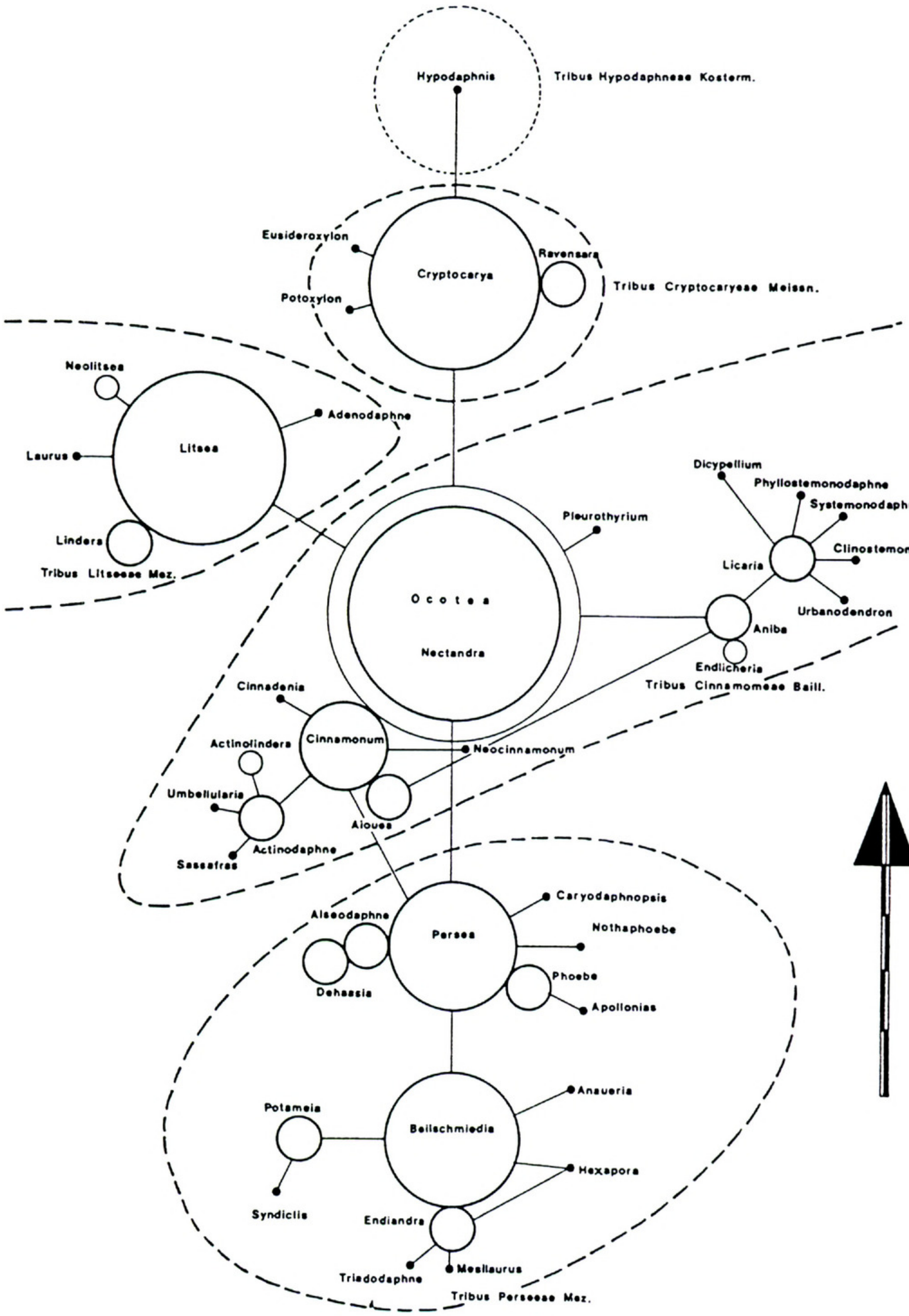

Figure 7. Classification of Kostermans (1957). Reprinted with permission.

used with some hesitation, no formal classification was proposed. Keys to genera were recently published by van der Werff (1991; for genera of the New World) and Rohwer (1993b; for genera worldwide).

Strength of Characters Used in Published Classifications

A robust classification demands that the characters used are reliable; that is, there are no or few

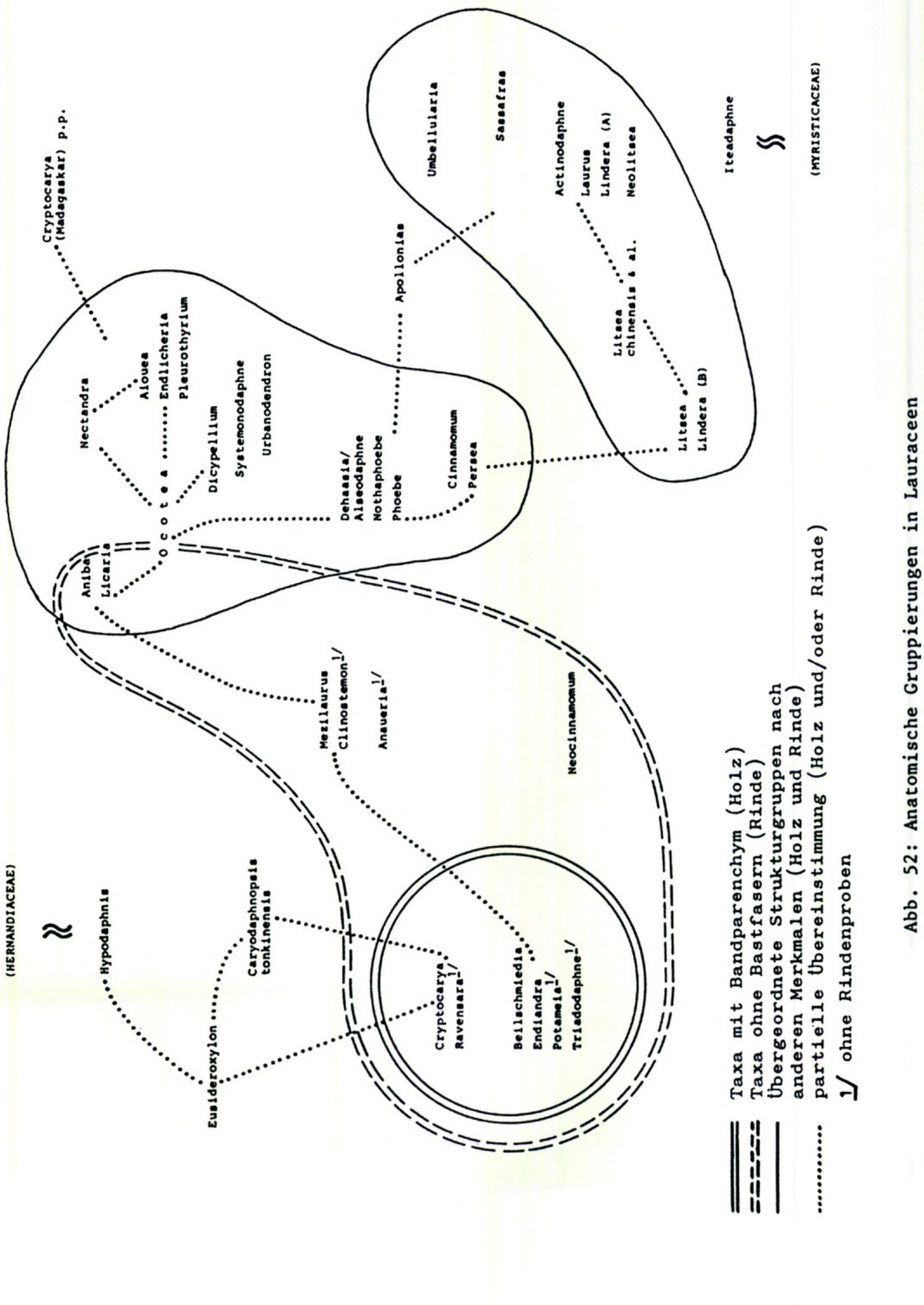

Figure 8. Classification of Richter (1981).

Table 1. Genera with variation in number of anther cells.

Aiouea	normally nine 2-celled, rarely six or three 2-celled
Aniba	normally nine 2-celled, rarely six 2-celled
Aspidostemon	either six 2-celled or three 2-celled
Beilschmiedia	normally nine 2-celled, rarely six 2-celled or nine 1-celled
Caryodaphnopsis	normally nine 4-celled, rarely nine 2-celled or six 2-celled
Cassytha	normally nine 2-celled, rarely six 2-celled
Cinnamomum	normally nine 4-celled, rarely nine 2-celled
Endiandra	normally three 2-celled, rarely six 2-celled
Endlicheria	normally nine 2-celled, rarely six 2-celled + three 4-celled
Kubitzkia	nine 2-celled or six 4-celled + three 2-celled
Persea	normally nine 4-celled, rarely nine 2-celled or six 4-celled + three 2-celled
Potameia	normally four 2-celled, rarely four 1-celled or two 1-celled
Urbanodendron	normally nine 4-celled, rarely nine 2-celled

exceptions to the conditions characteristic for a given taxon. An analysis of the characters used most frequently in the generic and suprageneric classifications of Lauraceae will allow us to estimate how well these taxa are founded.

One frequently used character refers to the inflorescence. It is phrased in slightly different ways in the various classifications. Nees (1836) and Meissner (1864) contrasted umbellate versus paniculate inflorescence, with and without an involucrum; Hutchinson (1964) stressed the presence or absence of bracts; Kostermans (1957), decussate bracts; and Rohwer (1993b) mentioned "some kind of involucre." Based on the senior author's experience, the character states of involucrate, racemose versus exinvolucrate, paniculate inflorescence are reliable; we know of no genera in which both kinds of inflorescence are represented, and we accept the inflorescence differences as reliable generic characters. The importance of inflorescence types in the classification of Lauraceae will be discussed further in this article.

The next set of frequently used characters are those of the androecium, i.e., the number of fertile stamens and number of anther cells on each stamen. Possible variation of these characters can, of course, best be studied in genera defined by something other than these androecial characters. This variation is considerable (Table 1). For instance, among the neotropical species of *Caryodaphnopsis*, defined by having opposite leaves and unequal tepals, are species with nine 4-celled stamens, nine 2-celled stamens, and six 4-celled stamens plus three staminodia. Likewise, most species of *Potameia*, defined by having dimerous flowers, have four 2-celled stamens; a few have four 1-celled stamens and one species, as yet undescribed, has two 1-celled stamens. Neotropical species placed in *Persea* mostly have nine 4-celled stamens, but some have nine 2-celled stamens or six 4-celled and three 2-celled or six 4-celled and three staminodia. Looking at the genera defined by 2-celled stamens, the similarity between most *Aiouea* species (2-celled) and *Cinnamomum* (4-celled) is striking and seems more than convergence; however, *Aiouea vexatrix* van der Werff is very similar to some sympatric *Ocotea* species, as are *A. lundelliana* Allen and *A. costaricensis* (Mez) Kostermans (van der Werff, 1987a, 1988; Rohwer et al., 1991). A similar situation is found in *Endlicheria* (two-celled). Some of its species are strikingly similar to *Rhodostemonodaphne* or *Ocotea* species (Rohwer et al., 1991). A third generic pair is formed by *Mezilaurus* (2-celled) and *Williamodendron* (4-celled); species of *Williamodendron* were initially described as *Mezilaurus* (van der Werff, 1987), but were subsequently recognized as a distinct genus (Kubitzki & Richter, 1987). A few other examples are presented in Table 2. On the other hand, there are also 2-celled genera that do not have a 4-celled counterpart, such as *Cryptocarya*, *Beilschmiedia*, *Aniba*, and *Licaria*. These examples indicate that the androecial characters often vary within genera and are

Table 2. "Genus" pairs in which apparently closely related species or species groups are placed in different genera due to generic circumscription by anther cell number.

4-celled	2-celled
Cinnamomum	*Aiouea*
Cinnamomum	*Temmodaphne*
Ocotea	*Aiouea*
Ocotea	*Endlicheria*
Rhodostemonodaphne	*Endlicheria*
Williamodendron	*Mezilaurus*
Litsea	*Lindera*
Parasassafras	*Sinosassafras*

unreliable characters in classification at generic and higher levels.

The only character of the gynoecium frequently used is the degree to which the fruit is covered by the hypanthium—from no cover and fully exposed to a completely inferior ovary and the fruit fused with the hypanthium. In most genera this character is constant; exceptions occur in *Ocotea*, which includes species with pronounced cup-shaped cupules and species with very small, platelike cupules. In general though, the gynoecium character promises to be useful in generic and suprageneric classifications, because of its constancy at the generic level.

Earlier classifications were attempts to order the taxa being studied and were, in fact, frequently keys translated into a hierarchical system. A classification was a system enabling one to make identifications, and if that goal was met, the classification was acceptable.

More recently, the idea that classifications should reflect relationships and evolution of the taxon to be classified has found wide acceptance. Whether or not a phylogenetic classification is helpful in the identification process is less important. It is important to be aware of the dual purpose of a classification—on the one hand a path to identification, on the other a reflection of the phylogeny. For purposes of identification, the androecial characters are very useful because they are well defined and readily observed. On the other hand, characters such as number of stamens or number of anther cells are variable in several genera. This can only be observed in genera that can be defined by other characters. For instance, *Caryodaphnopsis* can be recognized by having opposite leaves and strongly unequal tepals; it also has very distinct wood anatomical characters. Within *Caryodaphnopsis* are species with nine 4-celled, nine 2-celled, and six 2-celled stamens. Other genera, for example, *Ocotea*, lack non-androecial characters (*Ocotea* is defined by having nine 4-celled stamens, with the cells in two horizontal rows), and species that resemble *Ocotea* very closely, but with 2-celled instead of 4-celled stamens, are placed in different genera (van der Werff, 1988; Rohwer et al., 1991). Genera such as *Caryodaphnopsis,* whose species share several non-androecial characters, can be expected to be monophyletic, but genera such as *Ocotea,* whose species only share androecial characters, are not likely to be monophyletic. Problems with classification of Lauraceae exist at two levels: there is a need for better defined, monophyletic genera, and a need for a phylogenetic classification at the suprageneric level. The focus of the rest of this paper is a more natural classification at the suprageneric level; it is acknowledged that this will not immediately lead to monophyletic genera, or to easier identifications.

Outlook for a Phylogenetic Classification

As has been discussed, the existing classifications are largely based on floral characters. The androecial characters vary frequently within genera and are therefore a poor choice as main characters for a generic and suprageneric classification. The gynoecial character emphasized by Kostermans does not vary within genera and holds more promise. However, the classification based on this character differs greatly from the generic groupings using wood and bark anatomy.

It seems unlikely that a thorough reexamination of floral and fruit characters will yield data with which a more robust classification can be constructed. Incorporating new data sets in building a classification looks like a more promising approach. Such an approach requires extensive collaboration between participating specialists. A few years ago, such a project was proposed and initiated by B. Hyland and the senior author, and will incorporate data from DNA studies, wood and bark anatomy, leaf oils, leaf venation and leaf cuticles, fruit anatomy, pollen, inflorescence types, and the traditional flower and fruit morphology into a new classification.

The published results of the study of wood and bark anatomy by the junior author (Richter, 1981), and the senior author's observations of inflorescence structures, both indicate that the Lauraceae are divided into three groups of genera. Wood and bark features employed are of an exclusively qualitative nature, quantitative characters being excluded as less reliable for their intrinsically high variation. They were selected and weighted in a function of their diagnostic value (identification) and discriminatory power (classification) within the specific context of Lauraceae. The set of secondary xylem characters includes primarily those relating to axial parenchyma distribution, fiber morphology, inorganic compounds, and vessel morphology. Secondary phloem characters considered as highly diagnostic and discriminating refer mainly to mechanical tissues, i.e., presence versus absence and morphology of phloem fibers and sclereids. These features were employed both in the positive (present) and negative affirmative (absent) sense. Group definitions are never based on any single feature, but on a combination of lead characters supported by secondary features of lesser diagnostic and/or discriminatory value.

Figure 9. Inflorescence types of group 1.

In the following, observations on inflorescence types are described and complemented by evidence derived from wood and bark structure:

1. Tribe Laureae. A number of genera have a racemose inflorescence; each flower has one bracteole at the base of the pedicel. Frequently, the inflorescence axis is shortened, with the inflorescence appearing umbellate. The inflorescences are

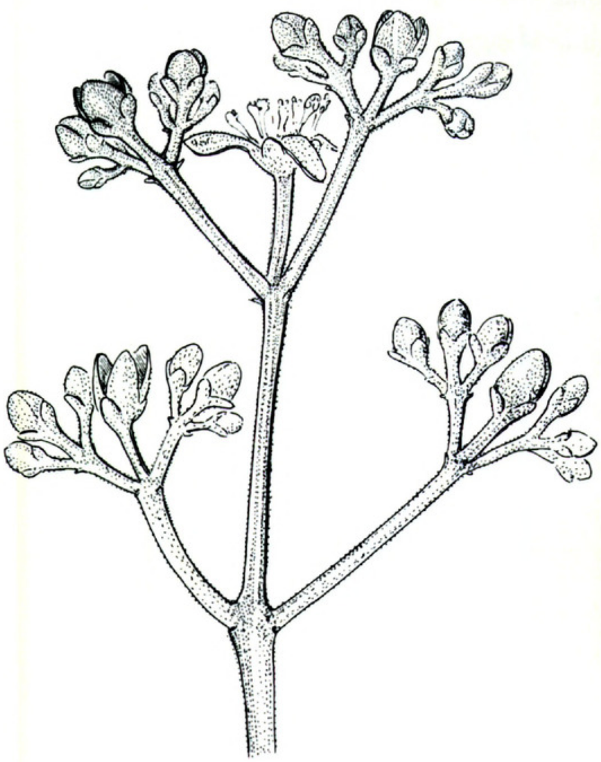

Figure 10. Inflorescence types of group 2.

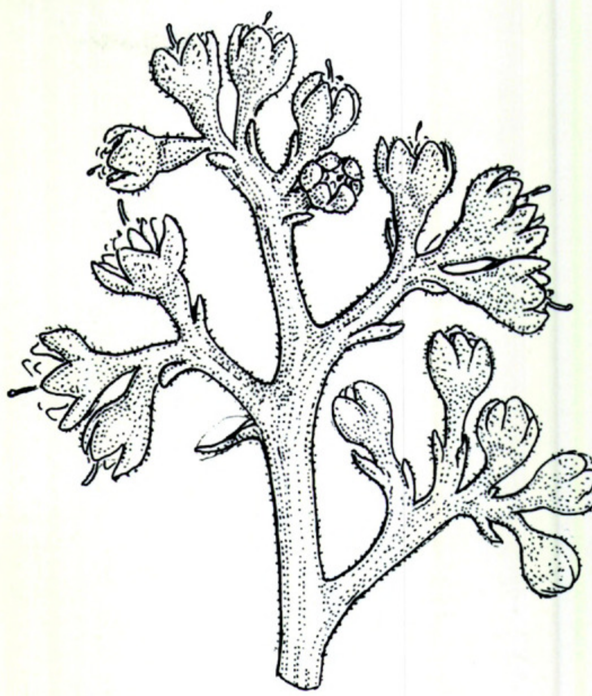

Figure 11. Inflorescence types of group 3.

often protected by a number of bracts (decussate or alternate). This group, with some modifications, has been recognized in nearly all classifications. It includes genera such as *Litsea, Lindera, Laurus,* and *Sassafras,* for instance (Fig. 9).

In terms of wood and bark structure, the group is characterized by the absence of marginal parenchyma and, in most instances, of septate fibers. Conversely, phloem fibers are always present. Further subunits can be recognized, for example the genus *Sassafras* on account of its accentuated growth ring structure, unique in Lauraceae and reflected in both secondary xylem ("ring porous") and phloem (distinct layering by early and late formed tissue strata).

2. Tribe Perseeae Nees. This group has a paniculate-cymose inflorescence. The initial branching of the inflorescence is paniculate, with alternate or opposite branches, while the flowers are arranged in cymes. The lateral flowers of a cyme are strictly opposite. At some point along the pedicel, two opposite bracts are present, frequently near the middle, but sometimes near the base. Included in this group are most neotropical genera (e.g., *Ocotea, Nectandra, Aniba, Licaria, Pleurothyrium*) and some neotropical/Asian genera (e.g., *Persea, Cinnamomum, Phoebe,* and *Dehaasia*) (Fig. 10).

Wood and bark structure depicts a group of genera characterized by the absence of marginal parenchyma and the ubiquitous presence of septate fibers (secondary xylem). Phloem fibers constitute part of the secondary phloem of nearly all taxa attributed to this group except some species of *Aniba, Licaria,* and *Ocotea* (Richter, 1981, 1985).

3. Tribe Cryptocaryeae Nees. The third group is formed by genera with a paniculate-± cymose inflorescence. At first glance these inflorescences look much like those of group 2, but the ultimate divisions are not strictly cymose. The lateral flowers of a "cyme" are not quite opposite, and flowers can appear individually placed along an inflorescence axis. The placement of bracts along the pedicels is variable in this group. Sometimes only one bract is present, sometimes two alternate or (sub)opposite ones; further observations are needed. This group includes such genera as *Beilschmiedia, Cryptocarya, Endiandra, Potameia,* and *Triadodaphne* (Fig. 11).

Wood and bark structure supports this circumscription of the *Beilschmiedia/Cryptocarya* assembly. All taxa share a number of distinctive features, such as the presence of marginal parenchyma, nonseptate fibers with conspicuously bordered pits, and exclusively simple vessel perforations in the secondary xylem. Conversely, in the secondary phloem the lack of fibers combines with characteristic sclereid formation.

As far as wood and bark structure is concerned, not all taxa can be satisfactorily accommodated in the three groups described above. *Cinnamomum* and *Persea,* for instance, appear to be transitional between Group 1 and Group 2, with closer affinities to the latter. Similarly, *Mezilaurus* (including *Clinostemon*), an easily defined and recognized taxon, shares diagnostic bark characters with Group 3 and diagnostic wood characters with Group 2. Other, mostly small genera with a very distinctive wood and bark structure do not fit well with any of the three groups, though certain affinities can be recognized, for instance, in the case of *Caryodaphnopsis*, *Eusideroxylon/Potoxylon*, and *Hypodaphnis* with Group 3, of *Aspidostemon* and *Chlorocardium* with Group 2, and of *Iteadaphne* with Group 1.

Biogeographically, this division in three groups of genera is more logical than the generic alliances proposed in earlier classifications. The Laureae, with racemose inflorescences, are best represented, at the generic level, in the Northern Hemisphere (*Laurus, Sassafras, Umbellularia, Parasassafras, Litsea, Lindera, Neolitsea*), although several genera are well represented in the Asian tropics and a few extend into Australia. Most genera with unisexual flowers (about 10) belong to this group, and it includes genera with four and two anther cells. The Perseeae are mostly neotropical, with the genera in the *Persea–Cinnamomum–Phoebe* complex also present in tropical and subtropical (Northern Hemisphere) Asia; *Ocotea* is also present in Africa and Madagascar. Only three genera in this group have unisexual flowers; one of these, *Ocotea*, also includes many species with bisexual flowers. Both genera with 2-celled and 4-celled stamens are part of this group. The Cryptocaryeae are best represented in the Southern Hemisphere (*Cryptocarya, Beilschmiedia, Endiandra, Potameia*), but are also present in the Northern Hemisphere. All genera in this group have bisexual flowers. The core genera (*Cryptocarya, Beilschmiedia, Endiandra, Potameia, Triadodaphne*) have all 2-celled stamens; *Hypodaphnis, Eusideroxylon*, and *Potoxylon*, provisionally placed in this group, have 4-celled anthers.

Although not all genera can be satisfactorily placed in Richter's system, it avoids several anomalies present in Kostermans's classification, such as treating *Endiandra, Mezilaurus, Persea*, and *Beilschmiedia* as close relatives.

Thus, the two recent classifications of Lauraceae differ greatly from one another. Kostermans's (1957) classification is based mainly on one character only, the position of the gynoecium relative to the hypanthium, while Richter's (1981) classification is based on several characters from bark and wood and is supported by observations on inflorescence types. Although not all genera can be placed in our proposed tribal groupings (data are not yet available for some small genera and some genera have small, few-flowered inflorescences, making an interpretation of the inflorescences difficult), the fact that two greatly different sets of data support this classification makes this the best classification at hand, and the one to be tested when additional data become available.

Literature Cited

Bentham, G. & J. D. Hooker. 1880. Laurineae. Pp. 146–168 *in* G. Bentham & J. D. Hooker, Genera Plantarum, vol. 3. L. Reeve, London.

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

Hyland, B. P. M. 1989. A revision of Lauraceae in Australia (excluding *Cassytha*). Austral. Syst. Bot. 2: 135–267.

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

Kubitzki, K. 1982. Lauraceae: *Aniba*. Fl. Neotrop. Monogr. 31: 1–84.

——— & H. G. Richter. 1987. *Williamodendron* Kubitzki & Richter, a new genus of neotropical Lauraceae. Bot. Jahrb. Syst. 109: 49–89.

Meissner, C. F. 1864. Lauraceae. *In:* A. de Candolle (editor), Prodromus Systematis Naturalis 15: 1–260.

Mez, C. 1889. Lauraceae Americanae. Jahrb. Königl. Bot. Gart. Berlin 5: 1–556.

Nees von Esenbeck, F. C. G. D. 1836. Systema Laurinarum. Sumtibus Veitii et sociorum, Berlin.

Pax, F. 1889. Lauraceae. Pp. 106–126 *in* A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien, vol. III. Engelmann, Leipzig.

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

———. 1985. Wood and bark anatomy of Lauraceae II. *Licaria* Aublet. IAWA Bull. n.s. 6: 187–199.

Rohwer, J. G. 1993a. Lauraceae: *Nectandra*. Fl. Neotrop. Monogr. 60: 1–332.

———. 1993b. Lauraceae. Pp. 366–391 *in* K. Kubitzki, J. G. Rohwer & V. Bittrich (editors), The Families and Genera of Vascular Plants II. Springer-Verlag, Berlin.

———, H. G. Richter & H. van der Werff. 1991. Two new genera of neotropical Lauraceae and critical remarks on the generic delimitation. Ann. Missouri Bot. Gard. 78: 388–400.

Werff, H. van der. 1987a. Six new species of neotropical Lauraceae. Ann. Missouri Bot. Gard. 74: 401–412.

———. 1987b. A revision of *Mezilaurus* (Lauraceae). Ann. Missouri Bot. Gard. 74: 153–182.

———. 1988. Eight new species and one new combination of neotropical Lauraceae. Ann. Missouri Bot. Gard. 75: 402–419.

———. 1991. A key to the genera of Lauraceae in the New World. Ann. Missouri Bot. Gard. 78: 377–387.

———. 1993. A revision of the genus *Pleurothyrium* (Lauraceae). Ann. Missouri Bot. Gard. 80: 39–118.