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A BRIEF NOMENCLATURAL REVIEW OF GENERA AND TRIBES IN THEACEAE

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ABSTRACT

The angiosperm family Theaceae has been investigated extensively with a rich publication record of anatomical, cytological, paleontological, and palynological data analyses and interpretation. Recent developmental and molecular data sets and the application of cladistic analytical methods support dramatic changes in circumscription at the familial, tribal, and generic levels. Growing interest in the family outside the taxonomic and systematic fields warrants a brief review of the recent nomenclatural history (mainly 20th century), some of the classification systems currently in use, and an explanation of which data support various classification schemes. An abridged bibliography with critical nomenclatural references is provided.

Key words: anatomy, classification, morphology, nomenclature, systematics, Theaceae.

INTRODUCTION

Theaceae s.s. (APG I 1998; Prince and Parks 2001; APG II 2003; Stevens et al. 2004) are a flowering plant family of ca. 9 genera and up to 460 species that are most diverse in the subtropics and tropics, especially in the forests of Southeast Asia. Classifications such as those of Cronquist (1981) and Dahlgren (1983) circumscribed the family more broadly than more recent classification systems listed above, and placed the family within Ericales or Theales of Dilleniidae. The family includes economically important and well-studied plants such as the beverage tea (*Camellia sinensis*), cooking oil camellia (*Camellia oleifera*), and a number of woody ornamentals (*Camellia* spp., *Franklinia*, *Gordonia* spp., *Stewartia* spp., etc.). There is substantial medicinal interest in members of the family, especially in species of the genus *Camellia*, due to the potential of their compounds as curatives for some cancers, heart disease, and liver disorders (Hertog et al. 1993; Katiyar et al. 1993; Imai and Nakachi 1995). The primary compounds associated with the observed benefits of tea drinking are antioxidants such as flavonols and catechins (polyphenols), compounds especially abundant in green tea leaves. These are also the compounds that give tea its unique flavor.

Theaceous plants can be recognized by a suite of morphological characters including spiral arrangement of the perianth parts, several series of numerous stamens, and presence of involucre bracts that often grade into the sepals (Lawrence 1951). Unfortunately, each of the individual features can be found in representatives of other flowering plant families including Actinidiaceae, Pentaphragaceae, Symplocaceae, Ternstroemiaceae (sensu Weitzman et al. 2004), and Tetrameristaceae (sensu Kubitzki 2004). In a literature survey Tsou (1995) found no specific morphological char-

acters that were restricted to the family and could be used to circumscribe it. However, later developmental studies (Tsou 1997, 1998) identified the production of pseudopollen to be unique to members of Theaceae, currently the only known autapomorphy for the group.

As previously stated, Theaceae historically included many more taxa than currently circumscribed. Cronquist (1981) included ca. 40 genera and 600 species in the family Theaceae, distributed in the following four subfamilies: Asteropeiioideae, Bonnetioideae, Ternstroemioidae (including *Sladenia*), and Theoideae. Dahlgren (1983) included Pellicieraceae and Tetrameristaceae in the family, but excluded Bonnetiaceae. Takhtajan (1997) included subfamilies Sladenioidae, Ternstroemioidae, and Theoideae, while Goldberg (1986) and Thorne (1992) recognized *Sladenia* as a distinct monotypic family. The most recent treatment in Kubitzki (2004) restricts Theaceae to Cronquist's Theoideae. These are not the only classification systems currently available but they represent some of the most frequently cited systems and they are summarized in Table 1.

A recently published study of 60 morphological characters by Luna Vega and Ochoterena (2004) indicates that Theaceae s.s. are not a natural group (based on the consensus tree) and lack support (Jackknife <50%). This is not surprising given the number of taxa and characters. Additional non-molecular data (Beauvisage 1920; Keng 1962; Baretta-Kuipers 1976; Kvaček and Walther 1984a,b; Knobloch and Mai 1986; Grote and Dilcher 1989, 1992; Liang and Baas 1990, 1991; Tiffney 1994) could be analyzed in a phylogenetic context.

Analyses of nucleic acid data (Morton et al. 1996, 1997b; APG I 1998; Prince and Parks 2001; Anderberg et al. 2002) support the most restrictive circum-

Table 1. Recent classification systems of Theaceae sensu lato and other potentially related members of Theales (or Ericales).

Cronquist 1981	Dahlgren 1983	Goldberg 1986	Thorne 1992	Takhtajan 1997	Kubitzki 2004
THEALES/ERICALES INCLUDE:					
Theaceae including: Theioideae Ternstroemiaceae [incl. <i>Sladenia</i> ?]	Theaceae including: Theioideae Ternstroemiaceae [incl. <i>Sladenia</i> ?]	Theaceae including: Theioideae Ternstroemiaceae [incl. <i>Sladenia</i> ?]	Theaceae including: Theioideae Ternstroemiaceae [incl. <i>Sladenia</i> ?]	Theaceae including: Theioideae Ternstroemiaceae Sladenioideae Asteropeiaceae Bonnetiaceae Pellicieraceae Pentaphylacaceae Medusagynaceae Tetrameristaceae Caryocaraceae	Theaceae s.s. Ternstroemiaceae [incl. Pentaphylacaceae] Sladeniaceae Pellicieraceae Tetrameristaceae Symplocaceae
Asteropeioideae Bonnetioideae Pellicieraceae Pentaphylacaceae Medusagynaceae Tetrameristaceae Caryocaraceae	[Asteropeiaceae?] Bonnetiaceae Pellicieraceae Pentaphylacaceae Medusagynaceae Tetrameristaceae Caryocaraceae	Asteropeioideae Bonnetiaceae Pellicieraceae Pentaphylacaceae Medusagynaceae Tetrameristaceae Caryocaraceae Symplocaceae	Asteropeiaceae Bonnetiaceae Pellicieraceae Pentaphylacaceae Medusagynaceae Tetrameristaceae Caryocaraceae Symplocaceae		
THEALES/ERICALES EXCLUDE:					
Symplocaceae	Symplocaceae			Symplocaceae	Asteropeiaceae Bonnetiaceae Medusagynaceae Caryocaraceae

scription of the family, including only Cronquist's (1981) subfamily Theioideae, as reflected by the classifications of the APG I (1998), Prince and Parks (2001), and APG II (2003). The classification of the APG I (1998) and APG II (2003) based on molecular phylogenies also place Ericales (or Theales) in a much more derived position than earlier classifications, nested at the base of Asteridae. Molecular data analyses and recent developmental studies support dramatic changes in tribal and generic circumscription as well (Tsou 1995, 1997, 1998; Yang 2000; Prince and Parks 2001; Prince 2002).

Growing horticultural and medicinal interest in the family warrants a brief review of the recent nomenclatural history and some of the classification systems in use. With this goal in mind, the circumscription of the family, tribes, and genera of Theaceae are discussed below with reference to the molecular, morphological, and developmental evidence supporting various classification systems. A list of all names of Theaceae listed here and their publication information is provided in Appendix A.

DISCUSSION

Familial Circumscription and Nomenclature

The name Theaceae (as order Theacées) was published in 1813 by Mirbel and included the same two genera, *Camellia* and *Thea*, first described by Linnaeus in 1753 (now considered synonymous by all authors). At the same time, Mirbel also published the name Ternstroemiaceae (as order Ternstromiées), which he distinguished from Theaceae based on anther insertion (basifixed versus versatile), anther shape, fruit dehiscence,

and a number of other macro- and microscopic characters. The family name Theaceae (versus Camelliaceae) is one of many names conserved following the creation of the Subcommittee for Family Names at the 9th International Botanical Congress (per Stafleu 1966). During the 10th International Botanical Congress the proposal of Bullock (*Nomina Familiarum Conservanda Proposita*; 1959) was voted on and, with a few exceptions, accepted (Stafleu 1966). Theaceae familial circumscription was first re-examined by Don (1825) and then by Lindley (1831) who included Theaceae within Ternstroemiaceae because "no solid difference exists between this last order [Ternströmiaceae] and Theacéæ," based on the work of Cambes-sédes (1828). This began a long history during which Theaceae became a general repository for plants with 5-merous flowers and many, fascicled stamens. Endlicher (1840) published one of the earliest familywide treatments (as Ordo Ternströmiaceae), recognizing four tribes and 22 genera. Bentham (1861) reviewed the major taxonomic treatments of the family (s.l.), providing a detailed discussion of characters and generic affinities. He followed that publication with a treatment of the family in *Genera Plantarum* (Bentham 1862) in which six tribes and 32 genera were recognized including several of those listed below.

Field (1993) lists five small families, Asteropeiaceae, Bonnetiaceae, Pellicieraceae, Pentaphylacaceae, and Tetrameristaceae that are "now generally accepted as being included in Theaceae." Contrary to Field's statement, only one of the major classification systems (Table 1) places Tetrameristaceae within Theaceae, and none includes Pentaphylacaceae. Investigations based

on molecular data provide compelling evidence for the exclusion of these families as well. Morton et al. (1997a) and Cuénoud et al. (2002) place Asteropeiaceae in the Caryophyllales. APG II (2003) and morphological data (Stevens et al. 2004) place Bonnetiaceae within Malpighiales while Pellicieraceae, Pentaphylacaceae, and Tetrameristaceae have been placed in Ericales, but not part of Theaceae. The placement of Pellicieraceae, Pentaphylacaceae, and Tetrameristaceae in Ericales, but not sister to, nor part of Theaceae was confirmed by the five-gene analyses of Anderberg et al. (2002).

Field (1993) also lists of number of other families, Caryocaraceae, Medusagynaceae, Stachyuraceae, and Symplocaceae, which might be included within Theaceae. Molecular data (*rbcL*, 18S, *atpB*; Soltis et al. 2000) place Caryocaraceae and Medusagynaceae in the Malpighiales. Stachyuraceae have been placed in the Rosids (*rbcL*, 18S, *atpB*; Soltis et al. 2000). Only Symplocaceae remain close to Theaceae, as a member of Ericales per Soltis et al. (2000), Anderberg et al. (2002), and Bremer et al. (2002) based on analyses of multiple molecular data sets.

The application of phylogenetic methods to morphological, anatomical, and molecular data (A. Weitzman pers. comm.; Prince 1998; APG I 1998; Soltis et al. 2000; Albach et al. 2001; Prince and Parks 2001; Anderberg et al. 2002; APG II 2003; Stevens et al. 2004) supports the recognition of a narrowly circumscribed Theaceae (except Luna and Ochoterena 2004 as discussed above) equivalent to Theoideae in the classifications in Table 1.

Tribal Circumscription, Characters, and Nomenclature

Selected classification systems published over the past 100 years (Table 2) demonstrate significant disagreement among taxonomists regarding relationships within tribes and subtribes of Theaceae. Much of the disagreement between early (Airy-Shaw 1936) versus later (Sealy 1958; Keng 1962) classifications is due, in part, to the heavy reliance by early workers on floral characteristics that display continuous variation, such as in the size, number, and degree of fusion of the bracteoles, sepals, and petals. These characters vary considerably from species to species within genera such as *Camellia* s.l and *Gordonia* s.l. Examples can be found that span the range of variation, e.g., flowers of *Camellia sinensis* var. *sinensis* with 2–3 bracteoles, 5–6 sepals abruptly distinct from the 7–8 petals, parts nearly to fully distinct, versus those of *C. wenshanensis* with 10 perules (= bracteoles + sepals, a gradual progression in size and shape) that are incompletely distinct from the petals. The classification systems of Sealy (1958) and Keng (1962) were more strongly in-

fluenced by fruit dehiscence and gross morphology, and seed characters such as the presence or absence of a wing and the amount of endosperm present. In the tribal classification systems referenced in Table 2, explanatory text is extremely limited or lacking entirely in treatments by Sealy (1958) and Takhtajan (1997). The remaining classification systems are discussed below.

Airy-Shaw (1936) discussed only a few specifics of his treatment for the [sub]family Theaceae. He commented on the work of Pitard (1902a,b), in which *Gordoniinae* was narrowly circumscribed, including only *Gordonia lasianthus* (L.) J.Ellis, *Franklinia*, and *Shima*. He stated, “only characters of external morphology are here mentioned, but those interested will find them strikingly corroborated in most instances by the anatomical evidence published by Pitard.” The taxonomic key he provided utilized floral and fruit characters. His *Camelliaceae* were characterized by a many-bracteated pedicel; sepals and petals not abruptly dissimilar and spirally arranged; and the fruit a capsule with a persistent columella. He distinguished two subtribes, *Camelliinae* and *Laplaceinae*, based on the wingless versus winged seeds, respectively, or the fruit drupaceous in *Pyrenaria*: *Laplaceinae*.

He also subdivided the second tribe, *Gordoniaceae*, into two subtribes, *Gordoniinae* and *Stewartiinae*. Members of *Gordoniaceae* generally had pedicels with a pair of bracteoles, and five abruptly distinct sepals and petals. Members of subtribe *Stewartiinae* were characterized by their leafy sepals, no central columella in the fruit, and seeds with narrow wings or without wings. Members of subtribe *Gordoniinae* bore rigid sepals, possessed a central columella in the fruit, and produced winged seeds (unwinged in *Franklinia*).

Keng (1962) reviewed many of the previous classification systems. He stated that Sealy’s (1958) use of fruit and seed characters was justified, but would have been better if it had been based upon a greater number of characters. Keng built on Sealy’s character list, including more detailed fruit and seed characters such as copious versus scanty endosperm and the lack or presence of a central columella, and added anatomical characters such as sclereid distribution in the leaf. His tribe *Stuartiaceae* [= *Stewartiaceae*] included *Hartia* and *Stewartia*, which he stated should be merged, maintaining *Hartia* only as a subgenus. He also stated that the wood, fruit and seed characters indicated this was the least specialized tribe in the subfamily. Keng’s tribe *Gordoniaceae* had fruits with a persistent central columella, seeds with a thin layer of endosperm, and a large straight embryo. The large tribe *Camelliaceae* had fruits with a central columella, unwinged seeds without endosperm, and a large embryo.

Melchior (1925) published a comprehensive review of the morphological and anatomical features of the

Table 2. Various classification systems of the 20th century for Theaceae sensu stricto. All caps indicate tribes, underlining indicates subtribes.

Melchior 1925	Airy-Shaw 1936	Sealy 1958	Keng 1962	Ye 1990	Takhajan 1997	Tsou 1998	Prince & Parks 2001
CAMELLIEAE	CAMELLIEAE	GORDONIEAE	CAMELLIEAE	THEEAE	THEEAE	CAMELLIEAE	THEEAE
<u>Camelliinae</u>	<u>Camelliinae</u>	<u>Camelliinae</u>	<u>Camelliinae</u>	<u>Camellia</u>	<u>Camellia</u>	<u>Camellia</u>	<u>Camellia</u>
<i>Camellia</i>	<i>Camellia</i>	<i>Camellia</i>	<i>Camellia</i>	PYRENARIEAE	<i>Tutcheria</i>	<i>Polyspora</i>	<i>Polyspora</i>
<i>Piquetia</i>	<i>Tutcheria</i>	<i>Pyrenaria</i>	<i>Stereocarpus</i>	<i>Tutcheria</i>	<i>Pyrenaria</i>	<i>Pyrenaria</i>	<i>Pyrenaria</i>
<i>Stereocarpus</i>	<i>Piquetia</i>	<i>Yunnanea</i>	<i>Piquetia</i>	<i>Pyrenaria</i>	GORDONIEAE	<i>Sinopyrenaria</i>	<i>Laplacea</i>
<i>Tutcheria</i>	<i>Stereocarpus</i>	<i>Tutcheria</i>	<i>Yunnanea</i>	<i>Parapyrenaria</i>	<i>Gordonia</i>	[<i>Laplacea</i> ?]	<i>Apterosperma</i>
<i>Stewartia</i>	<u>Laplacinae</u>	<u>Gordoniinae</u>	<u>Pyrenarinae</u>	GORDONIEAE	<i>Laplacea</i>	[<i>Parapyrenaria</i> ?]	GORDONIEAE
<i>Franklinia</i>	<i>Laplacea</i>	<i>Gordonia</i>	<i>Pyrenaria</i>	<i>Polyspora</i>	<i>Schima</i>	GORDONIEAE	<i>Franklinia</i>
<u>Gordoniinae</u>	<i>Polyspora</i>	<i>Laplacea</i>	<i>Tutcheria</i>	<i>Gordonia</i>	<i>Franklinia</i>	<u>Gordoniinae</u>	<i>Gordonia</i>
<i>Laplacea</i>	<i>Pyrenaria</i>	<u>Schiminae</u>	GORDONIEAE	<i>Laplacea</i>	STEWARTIEAE	<i>Apterosperma</i>	<i>Schima</i>
<i>Gordonia</i>	GORDONIEAE	<i>Stewartia</i>	<u>Gordoniinae</u>	SCHIMEAE	<i>Stewartia</i>	<i>Franklinia</i>	STEWARTIEAE
<i>Pyrenaria</i>	<u>Gordoniinae</u>	<i>Schima</i>	<i>Gordonia</i>	<i>Schima</i>		<i>Gordonia</i>	<i>Stewartia</i>
<u>Schiminae</u>	<i>Gordonia</i>	<i>Franklinia</i>	<i>Laplacea</i>	<i>Apterosperma</i>		<i>Schima</i>	
<i>Schima</i>	<i>Franklinia</i>	<u>Schiminae</u>	<u>Schiminae</u>	<i>Franklinia</i>		<u>Stewartiinae</u>	
<i>Hartia</i>	<i>Schima</i>	<i>Schima</i>	<i>Schima</i>	STEWARTIEAE		<i>Hartia</i>	
	<u>Stewartiinae</u>	<i>Franklinia</i>	<i>Franklinia</i>	<i>Stewartia</i>		<i>Stewartia</i>	
	<i>Stewartia</i>	<u>Stewartiinae</u>	<u>Stewartiinae</u>	<i>Hartia</i>			
		<i>Hartia</i>	<i>Hartia</i>				
		<i>Stewartia</i>	<i>Stewartia</i>				

family, recognizing 23 genera in six subfamilies. The treatment included lengthy discussions of each genus and of several morphological characters, such as embryo, fruits, and sclereid distribution. In contrast, Melchior's 1964 revision of the family was brief, recognizing 34 genera in the same six subfamilies. The revision was limited to a description of the family and a new classification system, with almost no discussion of the genera. Melchior did comment on the new classification and how it differed significantly in the arrangement of the genera relative to other works, namely that of Airy-Shaw (1936). The only additional insight he provided was a reference to the recently published morphological and anatomical work of Keng (1962). Although Kobuski offered no suprageneric classification of his own, his contributions are significant. He studied almost every genus in the family s.l., providing detailed nomenclatural reviews and frequently agreeing with the classification published by Melchior (1925). His publications in Theaceae s.s. include *Franklinia* (1951), *Gordonia* (New World; 1951), *Laplacea* (including bibliographical notes; 1947, 1949, 1950), *Polyspora* (as *Gordonia*, Old World; 1940), and *Stewartia* (1951).

Ye (1990a) recognized 12 genera in his classification of the family and included a tree depicting evolutionary relationships along with major morphological and anatomical characters that supported specific clades. He split the family into two lineages, one comprising Pyrenarieae + Theeae, and the other Gordonieae + Schimeae + Stewartieae. This division was based on characters such as the presence or absence of a wing on the seed. Theeae (*Camellia* only) was distinguished from Pyrenarieae (*Parapyrenaria*, *Pyrenaria*, and *Tutcheria*) by copious versus no endosperm and large, fleshy cotyledons versus crumpled, folded cotyledons. Gordonieae were distinguished from Schimeae and Stewartieae by their apically winged seed versus a marginal wing circling the seed. Ye discussed the morphological and anatomical features of the subfamily in great detail. His treatment of the genera agrees with the opinions of Chang (1963, 1976, 1979, 1981; Chang and Bartholomew 1984) in that he recognized rather narrowly defined genera, but he provided little new data for the old problem of tribal circumscription.

Few early taxonomists provided a clear history for the tribal names they used in their classification systems. The earliest publications (Linnaeus 1753; de Jussieu 1789) did not include tribal or other subordinal rank names. The nomenclatural history provided below represents many, but perhaps not all, relevant publications at the tribal and subtribal levels. Table 2 presents some examples of tribal circumscription.

Tribes Camellieae, Gordonieae, and Laplace[e]ae were first published by Candolle (1824). Melchior re-

duced each to the rank of subtribe (as Camelliinae and Gordoniinae) in 1925 while erecting an additional subtribe, Schiminiinae. He included Laplaceinae within Gordoniinae. Tribal rank for Camellieae was restored by Dumortier in 1829. Choisy (1855; validated in Schlechtendal 1856) added the tribe Stuartieae (= Stewartieae) and Miquel (1859) added the tribe Pyrenarieae. The tribe Theeae was published by von Szyszyłowicz in 1893. The only tribal name published in the 20th century was Schimeae (Ye 1990a). The subtribal names Laplaceinae and Stewartiinae were first published by Airy-Shaw (1936). Pyrenariinae was used by Keng in 1962, although he may not have been the first to do so.

There are only three phylogenetic studies which sample broadly enough to address relationships among tribes of Theaceae: Tsou (1998), Prince (1998), and Prince and Parks (2001). Additional data, such as from the pollen morphology studies of Wei and Dehgan (1996; not seen) and Wei et al. (1999) could be re-evaluated in a phylogenetic context. Tsou (1998) analyzed ten morphological and anatomical characters for one outgroup and three predefined ingroup taxa that are equivalent to tribes, therefore only relationships among tribes, not monophyly of tribes, can be addressed. Her data matrix could be recoded based on the exemplars studied and re-analyzed to address the monophyly of the tribes as well. Tsou recognized two tribes, Camellieae (= Theoideae; group I) and Gordonieae (Stewartiinae: group IIa, and Gordoniinae: group IIb). Prince (1998) collected data on 42 morphological and anatomical characters for 13 outgroup taxa and 56 ingroup taxa. Although most genera were supported as monophyletic, only two of the three tribes, Gordonieae and Stewartieae, were supported as monophyletic.

Generic Circumscription, Characters, and Nomenclature

Monotypic genera (e.g., *Apterosperma*, *Dankia*, *Stereocarpus*) have often been segregated out of larger genera, resulting in several probable paraphyletic groupings. In addition to *Ficalhoa* and *Franklinia*, five groups of genera will be discussed in detail below: *Camellia* s.l., *Gordonia* s.l., *Pyrenaria* s.l., *Schima* s.l., and *Stewartia* s.l. Each of these five groups has been divided into several different genera depending upon the inclination of the author.

Ficalhoa.—The monotypic *Ficalhoa* (type species *Ficalhoa laurifolia*) is a tropical African plant initially placed within Ericaceae (Hiern 1898). Anatomical studies by Deng and Baas (1991) indicate a close relationship with members of Theoideae (Theaceae), especially with *Camellia* s.l. and *Pyrenaria* s.l. *Ficalhoa* was formally transferred to Theaceae by Robson

(1962) and is listed as such in the Flore du Congo du Rwanda et du Burundi (Boutique 1967). It is the only genus of Theaceae on the African continent. The species reaches approximately 30 m in height, is evergreen with elliptical, serrate leaves, and bears small (<5 mm diameter) flowers in cymes. The flowers bear 15 stamens in fascicles of three, opposite the petals. The capsular fruit dehisces into five valves releasing the numerous, small (0.5–1.0 mm diameter) seeds. These characteristics are atypical for the subfamily Theoideae whose flowers generally bear more stamens, and fewer, larger flowers per inflorescence. The structure of the anther is also unusual, releasing pollen through an apical pore-like slit. I found no published chromosome counts for this species. Molecular data analyses by Anderberg et al. (2002) place *Ficalhoa* near *Sladenia* and *Pentaphylax*, all sister to the family Ternstroemiaceae. Ternstroemiaceae and Theaceae form separate clades, but relationships among several families including Ternstroemiaceae and Theaceae remain unresolved. Stevens and Weitzman (2004) contrast *Ficalhoa* with *Sladenia*, concluding the two share enough similarities to be grouped together in Sladeniaceae.

Franklinia.—The monotypic *Franklinia* is recognized by most authors as distinct from *Gordonia*. *Franklinia* is represented by *F. alatomaha*. It is believed to be extinct in the wild (Harper and Leeds 1937; Bozeman and Bozeman 1986) and is known almost exclusively from cultivation. Plants are likely the progeny of the only known (former) population near Ft. Barrington, Georgia, USA, along the Alatomaha River (Harper and Leeds 1937). Although it has been placed within *Gordonia* in the past (as either *G. alatomaha*, *G. franklini*, or *G. pubescens*), most literature of the 20th century (except Luna Vega and Ochoterena 2004) places it in the monotypic *Franklinia*. It is a multi-stemmed, deciduous shrub or small tree. It bears white, fragrant, 5-merous flowers with many stamens. The fruit is a globose to subglobose capsule that splits loculicidally from the apex and septicidally from the base, releasing the narrowly winged seeds from five locules. The capsule includes a central, persistent columella. Published chromosome counts for *Franklinia* are $n = 18$, $2n = 36$ (Santamour 1963; Rüdénberg 1964). Recent developmental and molecular data analyses (Tsou 1998; Prince and Parks 2001) place *Franklinia* in a clade with *Gordonia* and *Schima*.

Camellia s.l.—Linnaeus described one species each of *Thea* and *Camellia* (with two varieties) that were, in his sexual system, widely separated in different “orders.” Today both are considered members of *Camellia*. References to tea have been found in Chinese literature for over 2000 years. *Camellia s.l.* has a large number of historical synonyms (*Calpandria*, *Desmitus*,

Drupifera, *Kemelia*, *Sasanqua*, *Thea*, *Theaphylla*, *Tsia*, and *Tsubaki*) which will not be discussed here. Segregate genera that have been erected during the 20th century include *Camelliastrum*, *Dankia*, *Glyptocarpa*, *Kailosocarpus*, *Parapiquetia*, *Piquetia*, *Stereocarpus*, *Theopsis*, and *Yunnanea*.

Camelliastrum was described by Nakai in 1940 to accommodate six species from southern China (including Taiwan). The species transferred to *Camelliastrum* possess basifixed anthers with a narrow connective unlike the remaining species of *Camellia* (according to Tuyama 1980). Tuyama examined specimens of several of the transferred species. He found, without exception, anthers that were better considered versatile, as the anther moved freely, and a range of connective widths similar to that of *Camellia*.

Dankia is known only from a single species (*D. langbianensis*) and herbarium sheet (Poilane 18648) collected in Vietnam (Annam) by Poilane near B-dlé and Dankia, in Lang-biang, hence the name. This species was described by Gagnepain (1939) as a member of Bixaceae. Hô (1991) transferred *Dankia* to *Camellia* without explanation. Descriptions of the flower and fruit of *Dankia* are consistent with *Camellia* (sepals 5, petals 5, stamens numerous, fruit dehiscent with five valves and a central placenta).

Kailosocarpus and *Parapiquetia* were both invalidly published by Hu (1957) because the name protologue lacked generic descriptions. No one has validated or recognized the generic name *Kailosocarpus*, although *Parapiquetia* was considered a synonym of *Camellia* by Chang (Chang and Bartholomew 1984).

Piquetia was described by Hallier in 1921 to recognize a unique combination of characters in a single species, *Thea piquetiana*, from Vietnam. The small shrubs of this species (2–5 m tall) bear large leaves (29–42 cm long; Sealy 1958) and multiple flowers on short bracteate axillary shoots. In 1958, Sealy transferred *P. piquetiana* to *Camellia*, stating that a similar arrangement of flowers occurs in other members of *Camellia*, especially in *C. sinensis*, although he did create a new section to accommodate the transferred species.

In 1921 Hallier also created *Stereocarpus* for the transfer of *Thea dormoyana*. Sealy (1958) created a monotypic section within *Camellia* to accommodate his transfer of this species back to *Camellia* in 1958. *Camellia dormoyana* is native to Cambodia, Laos, and Vietnam. It is a small tree bearing large leaves (11–20 cm long × 4–8 cm wide; <http://www.efloras.org/>), 3–4 ovules per locule, and a 5-locular capsule. According to Sealy it was the 5-locular fruit (many camellias have 3-locular fruits) and the greater number of ovules per locule that Hallier believed warranted generic recognition. Sealy argued that the character combination

was found within *Camellia*, thus generic recognition of *Piquetia* was not warranted.

Theopsis was also created by Nakai in 1940 based on an extremely reduced raceme relative to the inflorescences of other species of *Camellia*. Nakai transferred 14 species of southern China and Japan to the new genus. More species were added to the genus by Hu (1965). Tuyama (1980) believed the inflorescence of *Theopsis* was not distinct, concluding the “racemose theory of Professor Nakai is apparently due to his erroneous interpretation. There is no authority to segregate *Theopsis* from *Camellia* at the generic level.”

Yunnanea (Hu 1956) is a segregate genus from *Camellia* known from Yunnan Province, China. The only species, *Y. xylocarpa*, is known from a single herbarium specimen. Hu (1956) described the genus based on the indehiscent fruit, a characteristic not found in *Camellia*. Chang transferred *Y. xylocarpa* back to *Camellia* in 1981. Tuyama (1984) supported the transfer of *Yunnanea* to *Camellia*, stating “the naked pedicel and indehiscent fruit . . . cannot be tenable.” Tuyama surmized that the indehiscent fruit of the type specimen was immature, and, if mature, would have dehisced like *Camellia* fruits despite Hu’s (1956) clear statement to the contrary: “At first sight, the fruit looks like an immature capsule not yet dehiscent. But it differs first from the genus *Camellia* in that it is subtended by large persistent coriaceous bracts and sepals. In one fruit it is found that at [the] base the thick exocarp [is] slightly dehiscent. But it is doubtful if the very thick woody exocarp will finally dehisce into distinct valves and fall apart.” Tuyama also pointed out that the illustration of *Yunnanea* in Hu (1956) depicts seeds that are rounded wedge-shaped, like the seeds of *Camellia*, further evidence against recognition of a separate genus.

Camellia is currently recognized as a broadly circumscribed genus, encompassing all the segregate genera listed above. The genus has been characterized as follows: evergreen trees or shrubs; flowers bisexual, solitary or 2–3 in axillary clusters toward the apex of branches (in the vegetative bud scales fide Sealy 1958) or rarely terminal, pedicellate although not always obviously so, subtended by two or more bracteoles; bracteoles persistent or deciduous, distinct or not from the sepals; sepals 5 if distinct from bracteoles; petals 5–12, usually connate at the base; stamens many and in 2–6 series, often connate and basally adnate to the petals (falling as a unit with the corolla in most species); ovary superior, compound, locules 3–5, ovules 3 or 4 (rarely 8) per locule; fruits capsular, valves 3–5, mostly dehiscent from the apex, valves remaining attached at the base, central columella (short in unilocular fruits) persistent; seeds large (up to 2 cm), globose or angular-globose, endosperm with high oil con-

tent (Chang and Bartholomew 1984); embryo small (ca. 0.5 mm) and straight, cotyledons 2 (rarely 3 or 4), large (up to ca. 2 cm), fleshy. Specific measurements listed above are based on the diagrams of *Camellia sinensis* seeds in Fig. 2 of Keng (1962) and may not be typical for the genus. The description of the seed here differs somewhat from the descriptions of Keng (1962) and Choisy (1855), which report that the seeds of *Camellia* lack endosperm and possess a large embryo with fleshy (oil and protein storage) cotyledons. Additional studies would add significantly to our understanding of the diversity of anatomy in this and many other genera.

Chromosome studies have found the base chromosome number (n) to be 15 with many instances of polyploidy ($2n = 45, 60, 75, 90,$ and 120 ; representative papers: Ackerman 1971; Bezbaruah 1971; Kondo 1972, 1977a, 1978; Kondo and Andoh 1980; Kondo et al. 1986, 1989, 1991; Gu et al. 1988, 1989, 1990a,b, 1991, 1992; Xiao et al. 1991; Zhou et al. 1991, 1992).

Chang and Bartholomew (1984) recognized approximately 230 species of *Camellia*. Additional species are still being described (e.g., Ninh and Hakoda 1998; Ming 2000), increasing the number to approximately 290 species, the majority of which occur in China. The number of species remains highly controversial with Ming and Bartholomew (http://flora.huh.harvard.edu/china/mss/volume12/Theaceae-CAS_final.htm) recognizing only 120 species. The genus is distributed from India east to Japan, and south to Malaysia and the Philippines.

A detailed study of leaf architecture of 108 species of *Camellia* (Sun and Ming 1995) provided evidence to group species into six groups. It is unclear how many samples per species were examined but the data could be transformed and re-analyzed in a phylogenetic context. As presented, the data support the classification system proposed by Ming (2000).

The only available molecular study of *Camellia* s.l. was conducted by Xiao (2001) using *rpb2* exon and intron data. He surveyed 149 samples of *Camellia* s.l. representing all 14 sections in Chang’s classification. The *rpb2* data analyses support a monophyletic *Camellia* s.l. and monophyly for several sections including *Chrysantha*, *Furfuracea*, *Paracamellia*, and *Thea*. Additionally, the inclusion of the newly described *C. vidalii* J.C.Rosmann (Rosmann 1999) in the genus remains questionable. A summary of Xiao’s findings is available on the worldwide web (www.jhnews.com.cn/gb/content/2003-03/02/content_158712.htm). Ki-Joong Kim (pers. comm.) is working on an ITS phylogeny for the genus, but results are not available at this time.

Gordonia s.l.—Keng discussed the nomenclatural history of *Gordonia* s.l. in his 1984 treatment of the ge-

nus for *Florae Malesianae*. *Gordonia* was created by Ellis (1771) for the only species occurring in the USA, *Gordonia lasianthus*. This genus was conserved over the older publication of *Lasianthus*, which was created for the species now treated as *Franklinia alatamaha*. In all subsequent discussion, *Gordonia* will refer only to *G. brandegeei* and *G. lasianthus*. Several additional generic names were published in the early 1800s, many of which were synonymized under *Gordonia* before 1900. These will be addressed under either *Laplacea* or *Polyspora* below. *Gordonia brandegeei* and *G. lasianthus* are columnar evergreen trees reaching 30 m in height. They bear shiny, toothed leaves. Flowers are produced in the leaf axils toward the ends of branches and are borne on a long (4–8 cm), flexible peduncle that is subtended by 4 bracteoles. The sepals and white petals are distinct and usually 5 in number. The ovary is topped by a single style (lacking in *G. brandegeei*) and a 5-lobed stigma. The fruit is a dry, loculicidally dehiscent, 5-valved capsule that houses 10–40 apically winged seeds. Santamour (1963) published a chromosome count of $2n = 30$ for *G. lasianthus* while Bostick (1965) reported $n = 18$. There are no known chromosome counts for *G. brandegeei*.

Laplacea is also a conserved name for a group of genera erected within a 4-year period: *Wikstroemia* (or *Wickstroemia* in some publications), *Lindleya*, and *Haemocharis*. These are all New World genera and are considered synonyms of *Laplacea* (and *Gordonia* by some authors). Originally, *Laplacea* was described for a specimen that appeared distinct from *Gordonia*. The peduncle was much shorter (<1 cm long), the sepals graded into the petals, and the ovary bore 5 free styles. As the number of plant collections from South America, Central America, and the Caribbean increased, the differences between *Gordonia* and *Laplacea* became less distinct. There is no debate over the inclusion of *Haemocharis*, *Lindleya*, and *Wikstroemia* in *Laplacea*. There are no known published chromosome counts for New World *Laplacea*. Approximately 20 New World species were recognized by Kobuski in his 1947 and 1950 reviews of the genus. Anna Weitzman (unpublished, pers. comm.) examined large numbers of specimens throughout the range and found that the variation in morphological characters, including those previously used to separate species, is continuous. Weitzman recognizes only two species (*Laplacea fruticosa* and *L. haematoxyloides*) in the New World.

Sweet (1831) published the name *Polyspora* for a species originally described as *Camellia axillaris*. Like *Laplacea*, *Polyspora* has a very short peduncle and perianth parts that grade from bracteole to sepal to petal, and does not appear to fall within the generic limits of *Gordonia*. Synonyms include *Antheëschima*, *Carria*, *Closaschima*, *Dipterospermum*, and *Nabiasodendron*. Significant nomenclatural difficulties remain

for species distributed in Asia. Old World species bear the generic name *Gordonia*, *Laplacea*, or *Polyspora*. None of the species currently included in *Polyspora* have ever been included within *Laplacea*, but members of both genera have been included within *Gordonia*. Chromosome counts of Old World species have been published for *G. excelsa* and *P. axillaris*; both have $2n = 30$ (Mehra 1972; Mehra and Sareen 1973). Oginuma et al. (1994) reported polyploidy ($2n = 90$) in *G. yunnanensis*. Keng recognized 21 species (as *Gordonia*) in his 1984 treatment for *Florae Malesianae*. Several species from China and Indochina increase the total number of Old World species to approximately 30 species.

Keng (1980b) recommended unifying *Gordonia*, *Laplacea*, and *Polyspora* under a more broadly defined *Gordonia*. He also identified evolutionary trends in the genus. The first was from undifferentiated or grading perianth parts to definitely numbered and clearly differentiated perianth parts. The second trend was in the degree of fusion of the style, from five free, slender styles to a single, stout style with a shallowly five-lobed stigma. Keng identified a few additional plausible trends of increasing staminal connation and adnation of the corolla, a reduction in the number of locules per ovary, and a reduction in peduncle length. As previously stated, Keng (1980b) concluded that there were no clear distinctions among the genera, and that the group was better treated as one large genus, with representatives in both the Old and New Worlds. Burkill (1917) and Sealy (1958) were of the same opinion.

Ye (1990b) disagreed strongly with the *Gordonia* s.l. proponents stating, “the genera have clear and definite limitation[s] in morphology.” He lists a number of characters including the differentiation and number of perule parts, anther attachment (versatile versus basifixed), degree of filament connation, style connation, number of locules, and pollen surface structure. He further stated that the least specialized genus is *Polyspora*, with *Gordonia* and *Laplacea* being more specialized. Melchior (1925, 1964), Kobuski (1950), and Backer and Bakhuizen (1963) also supported the separation of at least *Laplacea* from *Gordonia* (incl. *Polyspora*).

Molecular data analyses by Prince and Parks (2001) support the recognition of at least three distinct genera in this complex. *Gordonia* s.s. (*G. brandegeei* and *G. lasianthus*) were most closely related to *Franklinia* and *Schima* in *Gordonieae*. The 5 species of *Polyspora* sampled formed a monophyletic lineage within *Theaeae*, as did the 2 species of *Laplacea* sampled. Yang et al. (2004) confirmed the position of *Gordonia lasianthus* in *Gordonieae* and of *Polyspora* (5 species sampled) in *Theaeae* based on combined plastid, mitochondrial, and nuclear DNA sequence data.

Pyrenaria s.l.—*Pyrenaria* was established by Blume (1825–1826) for *P. serrata*, a species from Java. *Pyrenaria s.l.* includes two obvious cases of synonymy: *Dubardella* and *Eusynaxis*. Another synonym, *Glyptocarpa*, was discussed above under *Camellia*. *Eusynaxis* was based on *E. barringtonifolia* from India. Seemann (1859) transferred the species to *Pyrenaria* (*P. barringtonifolia*) without explanation.

Lam (1925) described the genus *Dubardella* and *D. kinabaluensis* as members of the Boerlagellaceae, an unusual family of plants from Sumatra that included two monotypic genera, *Boerlagella* and *Dubardella*. Airy-Shaw (1966) described the family Boerlagellaceae as, “an obscure and imperfectly known group, of very doubtful status.” He also indicated that *Dubardella* might be synonymous with *Adinandra* (Ternstroemiaceae). Keng (1976) reviewed the seed and embryo description from field notes of the type collection “seeds are mutually compressed, prominently scarred, with large and thin cotyledons twisted and contorted within the confinement of the seedcoat,” and concluded that the specimen was a member of *Pyrenaria*, although he was not willing to make an identification to species without viewing the type collection (*Clemens 10276*). Keng searched for the type specimen in Leiden (L), but was unable to locate it. Efforts to locate the specimen through direct contact or searches of on-line type databases at major herbaria (B, BR, CAS, HG, L, MICH, SING, UC, and US) have failed. Yang (2000) agreed with the treatment of *Dubardella* and *Eusynaxis*, listing them as synonyms of *Pyrenaria* in his revision of the genus.

Three additional taxa will be considered as potential sister genera to *Pyrenaria*, including *Parapyrenaria*, *Sinopyrenaria*, and *Tutcheria*.

Parapyrenaria was described by Chang (1963) for a new species endemic to Hainan, *P. hainanensis* H.T.Chang. *Parapyrenaria* differs from *Pyrenaria* in flower position (terminal versus axillary, respectively), deciduous bracteoles, greater number of sepals and petals (8–10), 3-locular ovary, simple style, 3-lobed stigma, and the elongated hilum of the seed. Chang transferred both *Parapyrenaria hainanensis* and *Tutcheria multisepala* to *Parapyrenaria multisepala* in 1979.

Hu erected *Sinopyrenaria* in 1956 for three species that shared characteristics with several different genera of Theaceae. The three species are distributed from south China east to Thailand. He was unsure of the affinities of this genus because: “The incompletely connate carpels with free styles and drupaceous fruit clearly show its close affinity to the Section *Mastersia* of the genus *Pyrenaria*, and also to the genera *Piquetia* and *Stereocarpus*. But the foliaceous bracteoles and sepals differ from those of the above genera and suggest those of *Hartia* and *Stewartia*. Altogether it is a

distinct new genus that I formerly erroneously referred to the genus *Pyrenaria* (Hu 1956).”

Tutcheria is the largest genus to be synonymized under *Pyrenaria* with approximately 10–15 species distributed throughout Southeast Asia, especially in warm temperate regions. *Tutcheria* was first established to accommodate *Camellia spectabilis*, based on a specimen from Hong Kong. Dunn (1908) allied *Tutcheria* to *Pyrenaria* but noted the differences in fruit dehiscence (indehiscent in *Pyrenaria* versus capsular in *Tutcheria*) and number of seeds per locule (2 in *Pyrenaria* versus 3–5 in *Tutcheria*). Study of subsequent collections of both *Pyrenaria* and *Tutcheria* from Southeast Asia by Keng (1972) identified a latitudinal gradient with regard to fruit dehiscence. The fruits are fleshy or leathery capsules, somewhat baccate or drupaceous. Species from more tropical habitats bear fruits that rot away while those from more temperate regions dry out and dehisce. Anatomical studies of seeds and seedlings by Keng (1972) led him to propose the reduction of *Tutcheria* to synonymy under *Pyrenaria*. Using embryological and palynological data Yang and Ming (1995a,b) reached the same conclusion.

Species of *Pyrenaria s.l.* are evergreen shrubs or small trees with alternate, simple leaves. Flowers are axillary (some appear terminal) with one or few flowers per axil, pedunculate (peduncle 0.6–1.5 cm) and subtended by bracteoles that may or may not be distinct from the calyx. Stamens are numerous (100–120), in 3–6 series, and are fused at the base and adnate to the corolla. The 3–5 fruit valves are deciduous, splitting loculicidally from the apex (and sometimes septically from the base). Two to five laterally compressed seeds are produced per locule, and there is a central, persistent columella. The fruit valves range in texture from dry to succulent. Keng (1980a) hypothesized that this variability might be an adaptation to delay seed germination or promote endozoochory. Bezbaruah (1971) published chromosome counts of $2n = 30$ for *Pyrenaria barringtonifolia*. Ackerman (1971) reported $2n = 30$ for *T. spectabilis* and $2n = 75$ for *T. virgata*. Oginuma et al. (1994) confirmed the count of $2n = 30$ for *T. spectabilis*. The genus is distributed throughout Southeast Asia and Indonesia. Keng (1980a) and Yang and Ming (1995a,b) recognized one broadly defined genus and Yang (2000) produced a subgeneric classification system as part of his dissertation thesis. Chang recognizes *Parapyrenaria*, *Pyrenaria*, and *Tutcheria*, but not *Sinopyrenaria*. Yang’s (2000) detailed revision of the complex provides morphological, cytological, and molecular evidence for the recognition of a single genus, *Pyrenaria*.

Schima s.l.—*Schima* was first published in 1823 (Reinwardt ex Blume 1823), but was invalid because the

genus and species lacked descriptions. The genus name was validly published two years later by Blume (1825–1826) for *Schima noronhae* Reinw. ex Blume. A vote by the members of the Committee for Spermatophyte Conservation of generic names of IAPT at a 1959 meeting (Keng 1994) confirmed the status of *Schima*. As was customary in the time before the type concept was established, Blume (1825–1826) did not designate a type. Farr et al. (1979) cite *S. excelsa* as the type but *S. excelsa* was later transferred to *Gordonia*. Clearly a number of nomenclatural problems remain. Schimas are (usually) evergreen trees that bear flowers singly or in small racemes borne terminally or in the axils of terminal leaves. The flowers are stalked, and the peduncle bears 2 bracteoles. The petals and sepals are distinct and (usually) 5 in number. Stamens are numerous and are arranged in 3–5 rows. The ovary is 5- (or 6–7)-locular and is topped by a single style with a 5-lobed stigma. Species of *Schima* are distributed throughout Asia.

Historically (1800s) many species of *Schima* were described under *Gordonia*. After significant realignments in the early 1900s, the generic limits of *Schima* were not questioned until 1976 when Chang described *Apterosperma oblata* from Guangdong Province, China. Chang stated that the new genus is near *Schima*, but with smaller flowers on shorter pedicels, stamens in two series, basifixed anthers, short styles, and a capsular fruit enclosing wingless, reniform seeds. These characteristics are very similar to *Schima*. The major difference between the two genera appears to be the number of staminal whorls (2 in *Apterosperma* versus 3–5 in *Schima*) and the wingless nature of the seed in *Apterosperma*.

Within *Schima* s.s., there has been significant debate as to the number of species that warrant recognition. Bloembergen (1952) regarded the genus as monotypic, recognizing one “complex-polymorphous” species, *Schima wallichii*, which he subdivided into nine geographically separated subspecies and three varieties. Mabberley (1987) adopted Bloembergen’s classification while Keng (1994) chose to recognize most of Bloembergen’s subspecies at the species level in his treatment for Flora Malesianae Precursores. Approximately 20 species of *Schima* and one species of *Apterosperma* have been described.

Relationships within *Schima* have not been addressed with molecular data. Chromosome data are available for *Schima* only, with reports of $n = 15$ (Malla et al. 1977) or $n = 18$ (Gill et al. 1984), $2n = 36$ (Bezbaruah 1971; Mehra 1972; Ono 1975, 1977). The $n = 15$ reports may be in error given the number of independent investigations reporting $n = 18$ and $2n = 36$. Molecular studies by Prince and Parks (2001) support the recognition of two distinct genera, *Apterosperma* in the tribe Theeae, and *Schima* in the tribe

Gordonieae. The placement of *Apterosperma* in the tribe Theeae was confirmed by the three-genome study of Yang et al. (2004) and contradicts the developmental data of Tsou (1998), where *Apterosperma* is placed within Gordonieae along with *Schima*.

Stewartia s.l.—*Stewartia* was first proposed in 1746 by Linnaeus (per Bryk 1954) for a Virginia coastal plain species (*S. virginica* = *S. malacodendron*), which he named in honor of the Earl of Bute, John Stuart (1713–1792). Linnaeus’s spelling of the genus as *Stewartia* was in error, but efforts to change the spelling of the genus name to *Stuartia* have been unsuccessful. Ironically, the Stuarts changed the spelling of their name from Stewart to Stuart in the 1500s (<http://www.electricscotland.com/history/nation/bute.htm>). According to www.ishipress.com/royalfam/royalfam.ged, “The change between Stewart and Stuart took place when Mary, Queen of Scots, married the Dauphin, later François II of France. The French spelled her surname “Stuart”, and when she returned, a widow, to Scotland, after 13 years in France, she kept the spelling, which her various half-siblings and cousins gradually adopted. She married one of the cousins, so her son was also a Stuart.” The correct spelling according to the International Code of Botanical Nomenclature (Greuter et al. 2000) is that of Linnaeus; however, some major references (e.g., Brummitt 1992) still use *Stuartia*. During the early exploration of the USA, independent discovery and description of the two New World species resulted in the description of three genera that are now considered synonyms of *Stewartia*: *Cavanilla*, *Malachodendron*, and *Stuartia*.

Stewartia s.l. is often split into two genera, *Hartia* (evergreen species) and *Stewartia* (deciduous species). *Hartia* was created by Dunn in 1902 for *H. sinensis*, a plant from Yunnan, China. Characteristics of the genus are the greater degree of connation of the anther filaments (into a staminal tube) and the greater number of seeds per locule than in species of *Stewartia*. Wu (1940) expanded the list of characteristics for the genus to include an evergreen habit and the presence of a conspicuously winged or inflated petiole that enclosed the terminal bud or lateral shoot. Cheng (1934), Yan (1981), and Ye (1982, 1984) maintain *Hartia*. Sixteen species of *Hartia* and 13 species of *Stewartia* are recognized by Ye (1982, 1984).

Chromosome counts show $n = 15$, $2n = 30$ for seven species of *Stewartia* s.l. (Santamour 1963). Published counts for the evergreen species do not conflict, despite confusion in the literature. Oginuma et al. (1994) published a count of $2n = 36$ for *H. sinensis*, citing Santamour’s earlier count of $2n = 30$. Santamour (1963) published a count of $2n = 30$ for *S. sinensis*. Thus this appears to be an error on the part of Oginuma et al., as *H. sinensis* is not a synonym of *S.*

sinensis, but rather of *S. pteropetiolata*. Yang's (2000) recent counts of $2n = 36$ for *H. sinensis* confirmed the earlier report by Oginuma et al. (1994). Clearly additional work needs to be done to determine if the species of *Hartia* and *Stewartia* differ in chromosome number.

Spongberg (1974) reviewed the deciduous species and found the evergreen habit to be the only reliable character to distinguish the two genera, a feature that he did not feel warranted generic distinction. Spongberg did not provide a subgeneric classification in his 1974 review, stating, "the species fail to fall into distinct subgeneric categories based on coherent groups of characters worthy of taxonomic recognition." Keng (1962) also recommended the merger of the two genera based on anatomical data, providing the following anatomical characteristics shared by *Hartia* and *Stewartia*, and that are absent from all other members of Theaceae he examined: nearly basal, axile placentation; ascending ovules; seeds with copious endosperm; and sclereids restricted to the petiole and petiole wing (versus throughout the leaf). Wu (1940) and Keng (1962) did not recognize *Hartia* at the generic level, but did recognize the evergreen species as a distinct subgenus. Li (1996) revised the genus *Stewartia* s.l., providing a detailed classification in which evergreen and deciduous species are dispersed into several subgenera, based on the degree of style connation, inflorescence type, and bracteole and sepal shape and size.

Stewartia s.l. can be distinguished from other members of Theaceae by its narrowly to broadly winged petioles and a capsular fruit that splits to reveal 2–4 narrowly winged or wingless seeds per locule. The fruit lacks a persistent central columella. Seeds are flattened and contain a small, straight embryo and copious endosperm. Results of molecular data analyses by Prince (2002) place *Hartia* within a larger *Stewartia* clade. Three data sets (two plastid and one nuclear) found the two North American species (*S. malacodendron* and *S. ovata*) to be more closely related to the evergreen species (*H. sinensis*, *H. villosa*, and *H. yunnanensis*) than to other deciduous species. A similar study by Li et al. (2002) found *Hartia* to be sister to the species of *Stewartia* that were sampled. Palynological studies by Heo and Lee (2004) indicate an intermediate position for *S. malacodendron* and *S. ovata*, evidence which could support either hypothesis. A study by Yang et al. (2004) confirm the placement of *Hartia* within a larger *Stewartia* clade based on plastid and mitochondrial DNA sequence data.

Significant advances have been made regarding familial, tribal, and generic circumscription in Theaceae, yet many questions remain. Conflicting anatomical, developmental, morphological, and molecular data only add to the taxonomic confusion regarding many taxa, such as *Hartia* and *Stewartia*. We now have more

tools available than ever before, and must employ them carefully, without preconceived notions of relationships. It is reassuring to find many hypotheses supported by molecular data, but many more unexpected relationships have arisen (e.g., *Apterosperma* in Theaceae, not Gordonieae). It is time to re-examine morphological and cytological characters in a phylogenetic context, and to be critical of unconfirmed results or those with poor statistical support. I hope this paper proves useful to both scientists and enthusiasts, and that it inspires more research into this diverse and popular group of plants.

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Appendix 1. Citation information for Theaceae sensu stricto.

Taxon name	Authority	Publication information			
		Author	Date	Volume/pages	Title
<i>Antheëschima</i>	Korth.	Korthals, P. W.	1842	3: 137	Verhandelingen over de natuurlijke geschiedenis der Nederlandsche overzeesche bezittingen, Botanie
<i>Apterosperma</i>	HungT.Chang	Chang, H. T.	1976	1976(2): 90	Acta Scientiarum Naturalium Universitatis Sunyatseni
<i>A. oblata</i>	HungT.Chang	Chang, H. T.	1976	1976(2): 91	Acta Scientiarum Naturalium Universitatis Sunyatseni
<i>Calpandria</i>	Blume	Blume, C. L.	1825	1: 178	Bijdragen tot de flora van Nederlandsch Indië
<i>Camellia</i>	L.	Linnaeus, C. von	1753	II: 698	Species Plantarum
<i>C. oleifera</i>	C.Abel	Abel, C.	1818	174, 363	Narrative of a journey in the interior of China
<i>C. sinensis</i>	(L.) Kuntze	Kuntze, O.	1887	x. 195 in obs.	Acta Horti Petropolitani
<i>C. spectabilis</i>	Champ. ex Benth.	Bentham, G.	1851	3: 310	Hooker's Kew Journal
<i>C. wenshanensis</i>	Hu	Hu, H. H.	1938	8: 130	Bulletin of the Fan Memorial Institute of Biology. Botany
Camelliaceae	DC.	Dumortier, B.-C.	1829	43, 47	Analyse des familles de plantes
Camelliaceae (as Camellieae)	DC.	Candolle, A. P. de	1816	978	Essai sur les propriétés médicales des plantes
<i>Camelliastrum</i>	Nakai	Nakai, T.	1940	12: 691	Journal of Japanese Botany
Camellieae	DC	Candolle, A. P. de	1813		Théorie élémentaire de la botanique, 2nd ed.?
Camellieae	(DC.) Dumort.	Dumortier, B.-C.	1829	47	Analyse des familles de plantes
Camel[1]iées (as subtribe)	M.Pitard	Pitard, M.	1902	57: 53	Actes de la Société Linnéenne de Bordeaux
Camelliinae	Melch.	Melchior, H.	1925	127	Die natürlichen Pflanzenfamilien
Camellioideae	Burnett	Burnett, G. T.	1835	827, 1120	Outlines of Botany
Camellioideae (as Camellidae)	Burnett	Burnett, G. T.	1835	827, 1120	Outlines of Botany
<i>Carria</i>	Gardner	Gardner, G.	1847	7: 6	Calcutta Journal of Natural History
<i>Cavanilla</i>	Salisb.	Salisbury, R. A.	1796	385	Prodromus stirpium in horto ad Chapel Allerton videntium
<i>Closaschima</i>	Korth.	Korthals, P. W.	1842	139	Verhandelingen over de natuurlijke geschiedenis der Nederlandsche overzeesche bezittingen, Botanie
<i>Dankia</i>	Gagnep.	Humbert, H.	1939	1: 198	Supplément à la flore générale de l'Indo-Chine
<i>D. langbianensis</i>	Gagnep.	Humbert, H.	1939	1: 198	Supplément à la flore générale de l'Indo-Chine
<i>Desmitus</i>	Raf.	Rafinesque, C. S.	1838	139	Sylva Telluriana
<i>Dipterospermum</i>	Griff.	Griffith, W.	1854	4: 564	Notulæ ad plantas asiaticas
<i>Drupifera</i>	Raf.	Rafinesque, C. S.	1838	140	Sylva Telluriana
<i>Dubardella</i>	H.J.Lam	Lam, H. J.	1925	7: 251	Bulletin du Jardin Botanique Buitenzorg (Bogor) III
<i>D. kinabaluensis</i>	H.J.Lam	Lam, H. J.	1925	7: 251	Bulletin du Jardin Botanique Buitenzorg (Bogor) III
<i>Eusynaxis</i>	Griff.	Griffith, W.	1854	4: 560	Notulæ ad plantas asiaticas
<i>E. barringtonifolia</i>	Griff.	Griffith, W.	1854	4: 560, 561	Notulæ ad plantas asiaticas
<i>Ficalhoa</i>	Hiern	Hiern, W. P.	1898	36: 329	Journal of Botany
<i>F. laurifolia</i>	Hiern	Hiern, W. P.	1898	36: 329	Journal of Botany
<i>Franklinia</i>	Bartram ex Marshall	Marshall, H.	1785	48	Arbustum Americanum
<i>F. alatomaha</i>	Bartram ex Marshall	Marshall, H.	1785	49	Arbustum Americanum
<i>Glyptocarpa</i>	Hu	Hu, H. H.	1965	10: 25, pls. III, IV	Acta Phytotaxonomica Sinica
<i>G. camellioides</i>	(Hu) Hu	Hu, H. H.	1965	x. 25	Acta Phytotaxonomica Sinica
<i>Gordonia</i>	J.Ellis	Ellis, J.	1770	60: 520, t. 11	Philosophical Transactions
<i>G. alatomaha</i>	(Marshall) Sarg.	Sargent, C. S.	1889	2: 616	Garden and Forest
<i>G. axillaris</i>	(Roxb.) A.Dietr.	Dietrich, A.	1847	863	Synopsis Plantarum
<i>G. brandegeei</i>	H.Keng	Keng, H.	1980	33(2): 310	Gardens' Bulletin Singapore
<i>G. excelsa</i>	(Blume) Blume	Blume, C. L.	1825	130	Bijdragen tot de flora van Nederlandsch Indië
<i>G. franklini</i>	L'Hér.	L'Héritier de Bruttelle, C. L.	1791	156	Stirpes Novae
<i>G. pubescens</i>	Cav.	Cavanilles, A. J.	1788	6: 308	Dessertatio Botanica
<i>G. yunnanensis</i>	(Hu)H.L.Li	Li, H. L.	1944	25: 307	Journal of the Arnold Arboretum
Gordoniaceae	(DC.) Spreng.	Sprengel, C. P. J.	1826	3: 12	Systema Vegetabilium
Gordonieae	DC.	Candolle, A. P. de	1824	527	Prodromus Systematis Naturalis Regni Vegetabilis

Appendix 1. Continued.

Taxon name	Authority	Publication information			
		Author	Date	Volume/pages	Title
Gordoniées (as tribe)	DC.	Choisy, J.-D.	1855	14: 135	Mémoires de la Société de Physique et d'Histoire Naturelle de Genève
Gordoniinae	(DC.) Melch.	Melchior, H.	1925	135	Die natürlichen Pflanzenfamilien
Gordonioidae (as Gordonieae)	Burmeist.	Burmeister, H. C. C.	1837	343	Handbuch der Naturgeschichte, Berlin
Haemocharidées (as subtribe)	M.Pitard	Pitard, M.	1902	57: 53	Actes de la Société Linnéenne de Bordeaux
<i>Haemocharis</i>	Salisb. ex C.FP. Martius et Zuccarini	Salisbury, R. A.	1806	ad t. 56	Paradisus Londinensis
<i>Hartia</i>	Dunn	Dunn, S. T.	1902	28, t. 2727	Hooker's Icones Plantarum
<i>H. sinensis</i>	Dunn	Dunn, S. T.	1902	28, t. 2727	Hooker's Icones Plantarum
<i>H. villosa</i>	(Merr.) Merr.	Merril, E. D.	1938	19: 54	Journal of the Arnold Arboretum
<i>H. yunnanensis</i>	Hu	Hu, H. H.	1935	vi.: 169	Bulletin of the Fan Memorial Institute of Biology
<i>Kailosocarpus</i>	Hu	Hu, H. H.	1957	20: 170	Scientia (China)
<i>K. camellioides</i>	Hu	Hu, H. H.	1957	20: 170	Scientia (China)
<i>Kemelia</i>	Raf.	Rafinesque, C. S.	1838	138, 139	Sylva Telluriana
<i>Lacathea</i>	Salisbury	Salisbury, R. A.	1806	ad t. 56	Paradisus Londinensis
<i>Laplacea</i>	Kunth	Humboldt, F. W. H. A., A. J. A. Bonpland & K. S. Kunth	1821	5: 207	Nova Genera et Species Plantarum
Laplaceae (as Laplaceae)	DC.	Candolle, A. P. de	1824	526	Prodromus Systematis Naturalis Regni Vegetabilis
Laplaceinae	(DC.) Airy Shaw	Airy-Shaw, H. K.	1936	499	Royal Botanic Gardens, Kew, Bulletin of Miscellaneous Information
<i>Lasianthus</i>	Adans.	Adanson, M.	1763	2: 398	Familles Naturelles des Plantes
<i>Lindleya</i>	Nees	Nees, C. G. D.	1821	4: 299	Flora
<i>Malachodendron</i>	Mitch.	Mitchell, J.	1769	38	Dissertatio Brevis de Principiis Botanicorum et Zoologorum
<i>Michauxia</i>	Salisb.	Salisbury, R. A.	1796	386	Prodromus stirpium in horto ad Chapel Allerton vigentium
<i>Nabiasodendron</i>	M.Pitard	Pitard, M.	1902	57: liv	Actes de la Société Linnéenne de Bordeaux
<i>Parapiquetia</i>	Hu	Hu, H. H.	1957	20: 170	Scientia (China)
<i>Parapyrenaria</i>	H.T.Chang	Chang, H. T.	1963	8: 287, pl. 37	Acta Phytotaxonomica Sinica
<i>Piquetia</i>	(Pierre) H.Hallier	Hallier, H.	1921	39: 162	Beihefte zum Botanischen Centralblatt
<i>P. piquetiana</i>	(Pierre ex Lanesan) H.Hallier	Hallier, H.	1921	39: 162	Beihefte zum Botanischen Centralblatt
<i>Polyspora</i>	Sweet	Sweet, R.	1831	61	Sweet's Hortus Britannicus
<i>P. axillaris</i>	(Roxb.) Sweet	Sweet, R.	1831	61	Sweet's Hortus Britannicus
<i>Pyrenaria</i>	Blume	Blume, C. L.	1826	17: 1119	Bijdragen tot de flora van Nederlandsch Indië
<i>P. barringtoni-fofia</i>	Seem.	Seemann, B.	1859	7: 49	Bonplandia
Pyrenarieae	[Burnett?] Miq.	Miquel, F. A. W.	1859	492	Flora van Nederlandsch Indië
Pyrenarieae (as order)	Choisy	Choisy, J.-D.	1855	14: 171	Mémoires de la Société de Physique et d'Histoire Naturelle de Genève
Pyrenariées (as tribe)	[Burnett?]	Choisy, J.-D.	1855	14: 169	Mémoires de la Société de Physique et d'Histoire Naturelle de Genève
Pyrenariinae	[Burnett?] Keng	Keng, H.	1962	348	University of California Publications in Botany
Pyrenarioideae (as Pyrenariidae)	Burnett	Burnett, G. T.	1835	695, 1137	Outlines of Botany
<i>Sarosantha</i>	Korth.	Korthals, P. W.	1841	103	Verhandelingen over de natuurlijke geschiedenis der Nederlandsche overzeesche bezittingen, Botanie
<i>Sasanqua</i>	Nees	Siebold	1832	4: 13	Nippon
<i>Schima</i>	Reinw. ex Blume	Blume, C. L.	1823	80	Catalogus van eenige der markwaardigste zoo in- als uit-heemsche gewassen, te vinden in's lands plantentuin te Buitenzorg
<i>S. excelsa</i>	Blume	Blume, C. L.	1823	80	Catalogus van eenige der markwaardigste zoo in- als uit-heemsche gewassen, te vinden in's lands plantentuin te Buitenzorg

Appendix 1. Continued.

Taxon name	Authority	Publication information			
		Author	Date	Volume/pages	Title
<i>S. noronhae</i>	Reinw. ex Blume	Blume, C. L.	1823	80	Catalogus van eenige der markwaardigste zoo in- als uit-heemsche gewassen, te vinden in's lands plantentuin te Buitenzorg
<i>S. wallichii</i>	(DC.) Korth.	Korthals, P. W.	1842	143	Verhandelingen over de natuurlijke geschiedenis der Nederlandsche overzeesche bezittingen, Botanie
Schimeae	C.X.Ye	Ye, C.-X.	1990	29: 79	Acta Scientiarum Naturalium Universitatis Sunyatseni
Schimées	M.Pitard	Pitard, M.	1902	57: 52	Actes de la Société Linnéenne de Bordeaux
Schiminae	(M.Pitard) Melch.	Melchior, H.	1925	138	Die natürlichen Pflanzenfamilien
<i>Sinopyrenaria</i>	Hu	Hu, H. H.	1956	5: 281	Acta Phytotaxonomica Sinica
<i>Sladenia</i>	R.F.Kurz	Kurz, R. F.	1873	11: 194, t. 133, f.1	Journal of Botany, British and Foreign
<i>Stereocarpus</i>	(Pierre) H.Hallier	Hallier, H.	1921	39: 162	Beihefte zum Botanischen Centralblatt
<i>S. dormoyana</i>	(Pierre ex Lanness.) H.Hallier	Hallier, H.	1921	39: 162	Beihefte zum Botanischen Centralblatt
<i>Stewartia</i>	L.	Linnaeus, C.	1753	II: 698	Species Plantarum
<i>S. malacodendron</i>	L.	Linnaeus, C.	1753	II: 698	Species Plantarum
<i>S. ovata</i>	(Cav.) Weath.	Weatherby, C. A.	1939	41: 198	Rhodora
<i>S. pteropetiolata</i>	W.C.Cheng	Cheng, W. C.	1934	202	Contributions of the Biological Laboratory of the Science Society of China, Botanical Series
<i>S. sinensis</i>	Rehder et E.H.Wilson	Rehder, A. and E. H. Wilson	1915	395	Plantae Wilsonianae
Stewartiinae	Airy Shaw	Airy-Shaw, H. K.	1936	499	Royal Botanic Gardens, Kew, Bulletin of Miscellaneous Information
<i>Stuartia</i>	L.	L'Héritier de Bruttelle, C. L.	1791	153	Stirpes novae aut minus cognitae
Stuartiées (= Stuartiæae/Stewartiæae)	Choisy	Choisy, J.-D.	1855	135	Mémoires de la Société de Physique et d'Histoire Naturelle de Genève
<i>Thea</i>	L.	Linnaeus, C.	1753	I: 515	Species Plantarum
Theaceae	Mirb.	Mirbel, C. F. B. de	1816	t. 112	Botanical Register
Theaceae	Ker Gawl.	Ker Gawler, J. B.	1816	2: ad t. 112	Botanical Register
Theaceae	D.Don	Don, D.	1825	224	Prodromus Florae Nepalensis
Théacées	Mirb.	Mirbel, C. F. B. de	1813	75: 382	Nouveau Bulletin des Sciences par la Société Philomatique
<i>Theaphylla</i>	Raf.	Rafinesque, C. S.	1830	267	Medical Flora; or, Manual of the Medical Botany of the United States
Theeae	Szyszył.	Szyszyłowicz, I. von	1893	180, 181	Die natürlichen Pflanzenfamilien
Théées (as tribe)	Szyszył.	Pitard	1902 ^b	57: 53	Actes de la Société Linnéenne de Bordeaux
Théinées (= Theeae)	Choisy	Choisy, J.-D.	1855	135	Mémoires de la Société de Physique et d'Histoire Naturelle de Genève
<i>Theopsis</i>	Nakai	Nakai, T.	1940	16: 704	Journal of Japanese Botany
<i>Tsia</i>	Adans.	Adanson, M.	1763	2: 450, 613	Familles des plantes
<i>Tsubaki</i>	Adans.	Adanson, M.	1763	2: 399	Familles des plantes
<i>Tutcheria</i>	Dunn	Dunn, S. T.	1908	46: 324	Journal of Botany, British and Foreign
<i>T. multisejala</i>	Merr. and Chun	Merrill, E. D. and Chun	1934	2: 41	Sunyatsenia
<i>T. spectabilis</i>	(Champ. ex Benth.) Dunn	Dunn, S. T.	1908	46: 324	Journal of Botany, British and Foreign
<i>T. virgata</i>	(Koidzm.) Nakai	Nakai, T.	1940	12: 708	Journal of Japanese Botany
<i>Wikstroemia</i>	Schrad.	Schrader, H. A.	1821	710	Göttingische Gelehrte Anzeigen
<i>Yunnanea</i>	Hu	Hu, H. H.	1956	5: 282	Acta Phytotaxonomica Sinica
<i>Y. xylocarpa</i>	Hu	Hu, H. H.	1956	5: 282	Acta Phytotaxonomica Sinica