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Leaf morphology and anatomy of *Camellia* section *Camellia* (Theaceae)

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The delimitations of species in *Camellia* section *Camellia* have been disputed for many years, resulting from uncertain relationships among species. Leaf morphological and anatomical characters for 54 species and three varieties in this section were investigated to reveal the relationships. Principal component analysis and cluster analysis were conducted using the transformed data for quantitative and qualitative characters from leaf morphology and anatomy. Combining the results of statistical analysis with comparative leaf characters of morphology and anatomy, we discussed the taxonomic treatment of section *Camellia* by Chang compared with that of Ming and we conclude that section *Camellia* consists of *c*. 50 species. © 2009 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2009, **159**, 456–476.

ADDITIONAL KEYWORDS: cluster analysis – epidermis – leaf anatomy – principal component analysis – taxonomy.

INTRODUCTION

Camellia section *Camellia* (L.) Dyer (Theaceae) is the largest section in the genus with about 60 species, subspecies and varieties (Chang, 1998), most of which are native to China. Some are cultivated as ornamental trees and are thus spread all over the world (Gao, Parks & Du, 2005). This section is characterized by large, usually red flowers and basal fusion of stamens (Gao *et al.*, 2005). Frequently, bracts and sepals are indistinguishable. The seeds of all species contain edible oils. There are three well-known taxonomic treatments of *Camellia* that have discussed the classification of species of this section in detail: Sealy (1958), Chang (1998) and Ming (2000). Sealy (1958) considered that this section contained eight distinct species. Chang (1998) suggested that it included 57 species and Ming (2000) revised it back to 12 species. There are many uncertainties about the relationships among species in this section and much disagreement among taxonomic treatments and further taxonomic research on this section is necessary.

Several works based on genetic information (Chen, Wang & Nelson, 2005; Yang *et al.*, 2006) have been conducted to clarify the interspecific relationships within genus *Camellia*, but these studies were not able to answer all the taxonomic questions.

On the one hand, leaf morphology and anatomy have always played an important role in plant taxonomy, particularly for identifying taxa in which variation in floral structures is uninformative or in which flowering specimens are infrequent owing to, for example, a limited flowering season (Meade & Parnell, 2003). On the other hand, leaf features have been largely unexploited in taxonomic studies, resulting from a belief that they respond in a plastic manner to environmental forces. In this study, all materials were taken from the International *Camellia* Species Garden in Jinhua city, making it possible to compare species growing under the same environmental conditions.

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In section *Camellia*, leaf morphology has been described in several publications (Chang, 1998; Ming, 2000; Gao *et al.*, 2005). However, a simple definition of leaf shape is difficult because of the extreme diversity observed. For example, the leaf shape of *Camellia hongkongensis* was described as oblong by Chang (1998), whereas Ming (2000) recorded it as oblong–elliptic, oblong or oblong–lanceolate and Gao *et al.* (2005) described it as oblong–elliptic. These differences in descriptions cause confusion and reduce the taxonomic value of leaf morphology. In contrast, a morphometrical analysis of leaf morphology is a useful and rapid method for identification of species. Recently, morphometric studies on *Taxus*, a taxonomically complex genus, with many sterile specimens like *Camellia*, showed that leaf characters are powerful in separating and identifying species in this morphologically labile plant group (Möller *et al.*, 2007; Shah *et al.*, 2008).

Epidermal characters have been considered to be of great use in studying relationships between taxa (Kong, 2001; Yang & Qi, 2005). In section *Camellia*, there are a few descriptions of leaf epidermal micromorphology (Ao, Chen & Chang, 2002; Ao, Ye & Zhang, 2007), but only a limited number of species were included. Thus, a more comprehensive investigation of leaf epidermal micromorphology in this section is necessary. The multiple epidermis (when present) and the presence or absence of stone cells provides useful information for taxonomy (Baranova, 1972). Additionally, the mesophyll usually offers some useful features, including the presence of crystals (Heintzelman & Howard, 1948). Nevertheless, in section *Camellia*, data for leaf characters in transverse sections are unavailable.

How to treat and make best use of morphological data in taxonomy is still a problem. A great many methods have been reported (Briggs & Walters, 1984; Kirchoff *et al.*, 2004; Plotze *et al.*, 2005; Kirchoff, Richter & Remington, 2007) and there are two main types of numerical techniques to represent taxonomic structure: clustering analysis and principal component analysis (PCA). The two techniques have been shown by Rhodes *et al.* (1971) to be complementary.

In summary, section *Camellia* is retained in the taxonomic treatments of genus *Camellia* by Chang (1998) and Ming (2000), but both the number and the delimitations of species in this section are controversial. This study aims to provide a basis for further investigations of systematic classification using the data of leaf morphology and anatomy.

MATERIAL AND METHODS

Leaf samples from 285 plants representing 54 species and three varieties in this section (according to Chang's taxonomic treatment) were collected from the International *Camellia* Species Garden in Jinhua city. Voucher specimens were deposited in Zhejiang Normal University (ZJNU) herbarium (Table 1). Five fully expanded sun-exposed leaves were sampled for each species.

Leaf epidermal scrapings were macerated in 40% sodium hypochlorite (NaClO) solution for 10 min at 35 °C. After removal of mesophyll tissues, pieces of epidermis were obtained and then dehydrated in an alcohol series and stained with safranin and fast green (Lü & Hu, 2001). Finally, they were mounted in neutral resin (Shanghai Shenhua Holdings Co., China) and examined with an Olympus BX50 light microscope (Olympus Co., Tokyo, Japan).

Shortly after being collected, leaves for transverse sections were cut into pieces and fixed in formaldehyde–acetic acid–alcohol (FAA) solution (Stern & Judd, 2002). Materials were dehydrated in a graded ethanol series, embedded in paraffin (Shanghai Shenhua Holdings Co.), sectioned with a KD-2508 Rotary Microtome (Zhejiang Jinhua Kedi Instrumental Equipment Co., China), treated with a safranin and fast-green stain procedure and mounted in neutral resin. The thicknesses of palisade tissues and spongy tissues were measured using the Dn-3 Micro-Image program (Ningbo Yongxin Optics Co., China). The terminology was based on the classification proposed by Metcalfe & Chalk (1979).

Ten leaves were sampled for each species and were scanned and estimated using the WinFOLIA system (Regent Instruments Inc., Canada). Measurements of area, perimeter, width, length, aspect ratio (width/length) and leaf form coefficient were averaged. All the average values for principal component analysis (PCA) were transformed using formula 1:

$$D_i = \frac{n\bar{X}_i}{\sum_{i=1}^{n} \bar{X}_i} \quad (1)$$

where D_i is the transformed value, $\bar{X}_i$ is the average value of one character of the i the species and n is the number of species examined. D_i is similar with Pearson's coefficient of variation (Briggs & Walters, 1984), making it possible to compare these data calculated in different units. Then a PCA was made using the PAST procedure (version 1.20) based on the transformed values (D_i). We chose the 'correlation (normalized var-covar)' option because the variables were measured in different units, necessitating normalization of all variables by division by their standard deviations. A scatter plot using the two most important components, component 1 (PC1) and component 2 (PC2) as the axes, was constructed.

Table 1. Vouchers of studied specimens, following the system of Chang (1998)

Taxa	Names of collectors and reference numbers	Date of collection
Camellia jinshajiangica Chang & S. L. Lee	*Peng Q. F. 200603601*	March 2006
Camellia omeiensis Chang	*Peng Q. F. 200603611*	March 2006
Camellia polyodonta How ex Hu	*Peng Q. F. 200603621*	March 2006
Camellia lanosituba Chang	*Peng Q. F. 200603631*	March 2006
Camellia longigyna Chang	*Peng Q. F. 200603641*	March 2006
Camellia lapidea Wu	*Peng Q. F. 200603651*	March 2006
Camellia phelloderma Chang, Liu & Zhang	*Peng Q. F. 200603661*	March 2006
Camellia mairei (Lévl.) Melch.	*Peng Q. F. 200603671*	March 2006
Camellia villosa Chang & S. Y. Liang	*Peng Q. F. 200603681*	March 2006
Camellia trichosperma Chang	*Peng Q. F. & Lin X. Y. 200604691*	April 2006
Camellia semiserrata Chi	*Peng Q. F. & Lin X. Y. 200604701*	April 2006
Camellia semiserrata var. *albiflora* Chang	*Peng Q. F. & Lin X. Y. 200604721*	April 2006
Camellia brevipetiolata Chang	*Peng Q. F. 200603731*	March 2006
Camellia phellocapsa Chang & B. K. Lee	*Peng Q. F. 200603742*	March 2006
Camellia compressa Chang & Wen ex Chang	*Peng Q. F. 200603751*	March 2006
Camellia magniflora Chang	*Peng Q. F. 200603761*	March 2006
Camellia lungshenensis Chang	*Peng Q. F. & Jiang B. 200610771*	October 2006
Camellia reticulata Lindl.	*Peng Q. F. 200603711*	March 2006
Camellia brevicolumna Chang, Liu & Zhang	*Peng Q. F. 200603781*	March 2006
Camellia pitadii Coh. St.	*Peng Q. F. & Jiang B. 200610801*	October 2006
Camellia pitardii var. *alba* Chang	*Peng Q. F. 200603811*	March 2006
Camellia pitardii var. *yunnaica* Sealy	*Peng Q. F. 200603821*	March 2006
Camellia xifongensis Y.K.Li ex X. C. Chen & F. Z. Zheng	*Peng Q. F. 200603831*	March 2006
Camellia hongkongensis Seem.	*Peng Q. F. 200603841*	March 2006
Camellia cryptoneura Chang	*Peng Q. F. 200603851*	March 2006
Camellia oviformis Chang	*Peng Q. F. 200603861*	March 2006
Camellia brachygyna Chang	*Peng Q. F. 200603871*	March 2006
Camellia tunganica Chang & B. K. Lee	*Peng Q. F. 200603881*	March 2006
Camellia bambusifolia Chang, Liu & Zhang	*Peng Q. F. 200603891*	March 2006
Camellia saluenensis Stapf ex Been	*Peng Q. F. & Jiang B. 200610901*	October 2006
Camellia albo-sericea Chang	*Peng Q. F. 200603911*	March 2006
Camellia bailinshanica Chang, Liu & Xiong	*Peng Q. F. 200603921*	March 2006
Camellia oligophlebia Chang	*Peng Q. F. 200603931*	March 2006
Camellia uraku (Mak.) Kitamura	*Peng Q. F. 200603941*	March 2006
Camellia edithae Hance	*Peng Q. F. & Jiang B. 200610961*	October 2006
Camellia paucipetala Chang	*Peng Q. F. 200603971*	March 2006
Camellia tenuivalvis Chang	*Peng Q. F. 200603981*	March 2006
Camellia boreali-yunnanica Chang	*Peng Q. F. 200603991*	March 2006
Camellia hibisciflora Chang	*Peng Q. F. 2006031001*	March 2006
Camellia concina Chang	*Peng Q. F. & Jiang B. 2006101011*	October 2006
Camellia glabsipetala Chang	*Peng Q. F. 2006031021*	March 2006
Camellia delicata Y. K. Li	*Peng Q. F. 2006031041*	March 2006
Camellia hunanica Chang & L. L. Qi ex Chang	*Peng Q. F. & Jiang B. 2006101051*	October 2006
Camellia glabriperulata Chang	*Peng Q. F. 2006031061*	March 2006
Camellia magnocarpa (Hu & Huang) Chang	*Peng Q. F. & Lin X. Y. 2006041081*	April 2006
Camellia liberistamina Chang & Chiu	*Peng Q. F. & Lin X. Y. 2006041091*	April 2006
Camellia lucidissima Chang	*Peng Q. F. 2006031101*	March 2006
Camellia chekiangoleosa Hu	*Peng Q. F. & Jiang B. 2006101111*	October 2006
Camellia mongshanica Chang & Ye	*Peng Q. F. 2006031121*	March 2006
Camellia japonica L.	*Peng Q. F. & Jiang B. 2006101131*	October 2006
Camellia rusticana (Honda) Kitamura	*Peng Q. F. & Jiang B. 2006101141*	October 2006
Camellia changii Ye	*Peng Q. F. & Jiang B. 2006101151*	October 2006
Camellia subintegra Huang ex Chang	*Peng Q. F. & Lin X. Y. 2006041161*	April 2006
Camellia lienshanensis Chang	*Peng Q. F. & Lin X. Y. 2006041171*	April 2006
Camellia crassissima Chang & Shi	*Peng Q. F. & Lin X. Y. 2006041181*	April 2006
Camellia apolyodonta Chang & Q. M. Chen	*Peng Q. F. & Lin X. Y. 2006041191*	April 2006
Camellia longicaudata Chang & Liang ex Chang	*Peng Q. F. & Jiang B. 2006102001*	October 2006

Table 2. Qualitative characters and character states

Pattern of anticlinal walls of adaxial epidermal cells	Straight–curved (1), repand (2), sinuous (3)
Pattern of anticlinal walls of abaxial epidermal cells	Straight–curved (1), repand (2), sinuous (3)
Hairs	Present (0), absent (1)
Cork wart	Present (1), absent (0)
Stomatal cluster	Present (1), absent (0)
Centre stomata	Present (1), absent (0)
Veins	Invisible (1), visible (2), raised (3)
Multiple epidermis	Present (1), absent (0)
Stone cells in mesophyll	Present (0), absent (1)

For the cluster analysis, all the measurements of quantitative characters (including leaf area, perimeter, width, length, aspect ratio, form coefficient, thickness of the upper and lower epidermis, thickness of palisade tissue and thickness of spongy tissue) were averaged and then transformed using formula 1. All the qualitative characters were given values (Table 2). A cluster analysis was conducted by PAST procedure (version 1.20) based on the data for quantitative characters and qualitative characters.

RESULTS

Characters of the epidermis

The characters of the leaf epidermis are listed in Table 3.

Epidermal cells

As seen under the light microsope (LM), the anticlinal walls of the epidermal cells appear straight–curved (Fig. 1), undulate (repand) (Fig. 2) or sinuous (Fig. 3). The patterns may vary between species or between the adaxial and abaxial epidermis of the same species (Table 3). Adaxial epidermal cells vary in size and (or) form even within the same specimen for 44 species (Figs 4–8). The adaxial epidermal cells of some species can be classified in more than one category. The abaxial epidermal cells usually share the same patterns within species. Sinuous anticlinal walls of the abaxial epidermal cells are found in 27 species (Fig. 9) and repand anticlinal walls of the abaxial epidermal cells are seen in 29 species (Fig. 10). Only one species has straight to curved anticlinal walls of the abaxial epidermal cells. Epidermal cells with walls are scarcely seen on the abaxial epidermis.

Stomatal apparatus

All species studied here are hypostomatic (i.e. with stomata only on the lower epidermis). Forty-three species have anisocytic stoma (Fig. 11, arrowhead), whereas the other species have one of two distinct types of stomatal apparatus (Figs 12–15). One is larger in size, infrequently distributed and surrounded by four or more subsidiary cells (Figs 13–15, arrow), defined as cyclocytic stomata by Metcalfe & Chalk (1979). The other is smaller and surrounded by three subsidiary cells which are variable in size, namely anisocytic stomata (Metcalfe & Chalk, 1979). Frequently, a few anisocytic stomata surround the larger, cyclocytic stomata in the form of a circle (Figs 13–15). Therefore, we define this cyclocytic stoma as the 'centre stoma' for its situation and significantly larger size (Table 4).

Stomatal clusters

In section *Camellia*, non-clustered stomata are found in nine species (Figs 16, 17). Stomatal clusters, in which two or more stomata are arranged adjacently with common subsidiary cells, have been documented in previous studies (Yang & Sack, 1995; Geisler, Yang & Sack, 1998; Tang *et al.*, 2002). In this study, 48 species have stomatal clusters, frequently involving 2–4 stomata (Figs 18, 19).

Hairs

A few species have hairs on the abaxial surface (Table 3). *Camellia edithae* has strikingly dense hairs and is thus distinguishable from other species. All of the hairs examined under LM are long, simple and unicellular. Their basal cells are usually stained red with safranin (Fig. 19).

Cork warts

Cork warts are of great diagnostic value (Sealy, 1958; Parks & Griffiths, 1963; Gao *et al.*, 2005). Only six species have cork warts and thus can be easily distinguished from other species (Fig. 20). These species are *C. lanosituba*, *C. compressa*, *C. magniflora*, *C. hibisciflora*, *C. japonica* and *C. rusticana* (Table 3). Cork warts are only present in the abaxial epidermis and their size is variable among species. On the fresh leaf surface, the cork warts look like brown spots. When examined under LM, they look like black pits surrounded by small fibrous epidermal cells, which are frequently stained red and thus easily distinguished from common epidermal cells.

Characters in transverse section

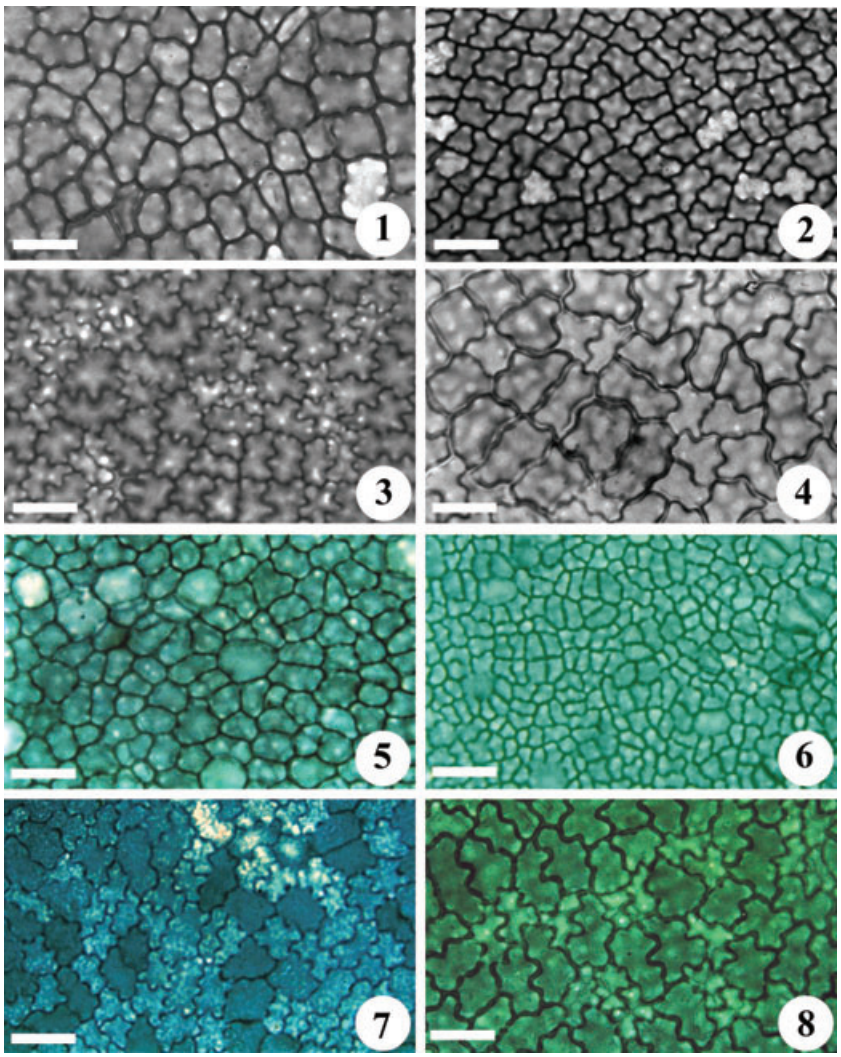
The characters in transverse section are shown in Table 5. (Detailed data of significance tests are listed in Supplementary Material, Appendix S1.)

Mesophyll

All species examined have bifacial leaves. The number of layers of palisade cells varies from species

Table 3. The characters of leaf epidermis

	Adaxial epidermis		Abaxial epidermis				
Taxa	VEC	POAWOEC	POAWOEC	Hairs	Cork warts	Stomatal clusters	Centre stomata
C. jinshajiangica	–	Repand	Sinuous	+	–	+	–
C. omeiensis	+	Repand	Sinuous	–	–	+	–
C. polyodonta	+	Repand	Sinuous	–	–	+	–
C. lanosituba	+	Repand	Sinuous	–	+	+	–
C. longigyna	+	Repand	Sinuous	–	–	+	–
C. lapidea	+	Repand	Repand	+	–	+	–
C. phelloderma	+	Repand	Repand	–	–	+	–
C. mairei	+	Repand	Sinuous	–	–	+	–
C. villosa	–	Repand	Sinuous	+	–	–	–
C. trichosperma	+	Str–cur	Repand	–	–	+	+
C. semiserrata	+	Str–cur	Repand	–	–	+	+
C. reticulata	+	Str–cur	Repand	–	–	+	–
C. semiserrata var. *albiflora*	+	Str–cur	Repand	–	–	+	+
C. brevipetiolata	+	Str–cur	Sinuous	–	–	+	+
C. phellocapsa	+	Str–cur	Sinuous	–	–	+	–
C. compressa	+	Sinuous	Repand	–	+	–	–
C. magniflora	+	Str–cur	Repand	–	+	–	–
C. lungshenensis	+	Str–cur	Sinuous	–	–	+	+
C. brevicolumna	–	Repand	Repand	–	–	–	–
C. pitardi	+	Repand	Repand	–	–	+	–
C. pitardii var. *alba*	+	Repand	Sinuous	–	–	+	–
C. pitardii var. *yunnanica*	+	Repand	Sinuous	–	–	+	–
C. xifongensis	+	str–cur	Sinuous	–	–	–	–
C. hongkongensis	+	str–cur	Sinuous	–	–	–	–
C. cryptoneura	+	Repand	Repand	–	–	+	+
C. oviformis	+	Sinuous	Sinuous	–	–	+	–
C. brachygyna	–	Sinuous	Sinuous	+	–	–	–
C. tunganica	+	str–cur	Sinuous	–	–	+	–
C. bambusifolia	–	str–cur	Repand	+	–	+	–
C. saluenensis	–	str–cur	Repand	+	–	+	–
C. albo–sericea	–	Repand	Sinuous	+	–	+	–
C. bailinshanica	–	Repand	Sinuous	+	–	+	–
C. oligophlebia	+	Sinuous	Sinuous	–	–	+	–
C. uraku	+	str–cur	str–cur	–	–	+	–
C. edithae	+	str–cur	Repand	+	–	+	–
C. paucipetala	+	Sinuous	Repand	–	–	+	–
C. tenuivalvis	–	Repand	Repand	–	–	+	–
C. boreali–yunnanica	–	Sinuous	Repand	–	–	+	–
C. hibisciflora	–	Repand	Repand	–	+	–	–
C. concina	–	Repand	Sinuous	–	–	–	–
C. glabsipetala	+	Sinuous	Sinuous	–	–	–	+
C. delicata	+	Sinuous	Sinuous	+	–	+	+
C. hunanica	+	Sinuous	Sinuous	–	–	+	–
C. glabriperulata	+	Sinuous	Sinuous	–	–	+	–
C. magnocarpa	+	str–cur	Repand	–	–	+	+
C. liberistamina	+	str–cur	Repand	–	–	+	+
C. lucidissima	+	str–cur	Repand	–	–	+	–
C. chekiangoleosa	+	str–cur	Repand	–	–	+	–
C. mongshanica	+	str–cur	Repand	–	–	+	+
C. japonica var. *japonica*	+	str–cur	Repand	–	+	+	–
C. japonica subsp. *rusticana*	+	str–cur	Repand	–	+	+	–
C. changii	–	str–cur	Repand	–	–	+	–
C. subintegra	+	str–cur	Repand	–	–	+	+
C. lienshanensis	+	str–cur	Repand	–	–	+	–
C. crassissima	+	str–cur	Repand	–	–	+	–
C. apolyodonta	+	str–cur	Sinuous	–	–	+	–
C. longicaudata	+	Sinuous	Sinuous	–	–	+	–



Figures 1–8. The characters of the adaxial epidermis under the light microscope. Figures 1–3. Showing the anticlinal walls of adaxial epidermal cells. Fig. 1. *C. changii*: straight-arched. Fig. 2. *C. tenuivalvis*: undulate (repand). Fig. 3. *C. paucipetala*: sinuous. Figures 4–8. Adaxial epidermal cells varying in size or form within the same species. Fig. 4. *C. villosa*. Fig. 5. *C. chekiangoleosa*. Fig. 6. *C. edithae*. Fig. 7. *C. glabsipetala*. Fig. 8. *C. glabriperulata*. Scale bar, 50 μm.

to species (Figs 21–24). In some species, it is difficult to differentiate palisade tissue from spongy tissue.

Apart from *C. changii*, all species have stone cells (Fig. 25). Frequently, these are present in palisade tissue and some of them penetrate into spongy tissue. Cluster crystals are present in all species.

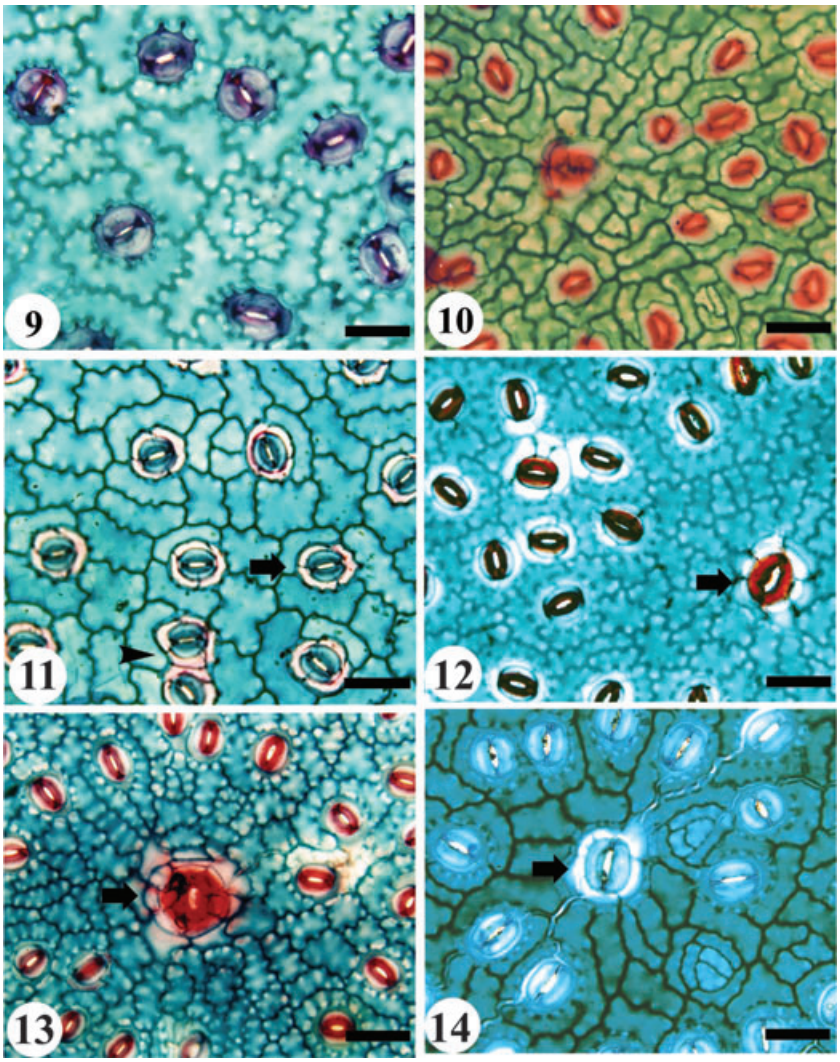
Epidermis

With the exception of those species with a single-layered epidermis, 44 species have a multiple epidermis (Table 5). Of these, only *C. japonica* has a multiple epidermis in which hypodermal cells are arranged adjacently without intercellular spaces (Fig. 26) and therefore it can be readily distinguished. Forty-three species have a discontinuous multiple epidermis (Fig. 27, arrow). Especially large epidermal cells, with few contents, are seen in some species (Fig. 28, arrow).

The transverse view reveals that the guard cells are not surrounded but slightly elevated by subsidiary cells (Fig. 29, arrow). In a few species, guard cells lie on two superposed subsidiary cells rather than a single subsidiary cell (Fig. 30, arrow). Both the basal cells of hairs (Fig. 31) and the cells in cork warts (Fig. 32) seem to be suberized.

Veins

Some diagnostic characters are found in veins. *Camellia japonica* has cork warts on the veins (Fig. 33) and is therefore different from other species.

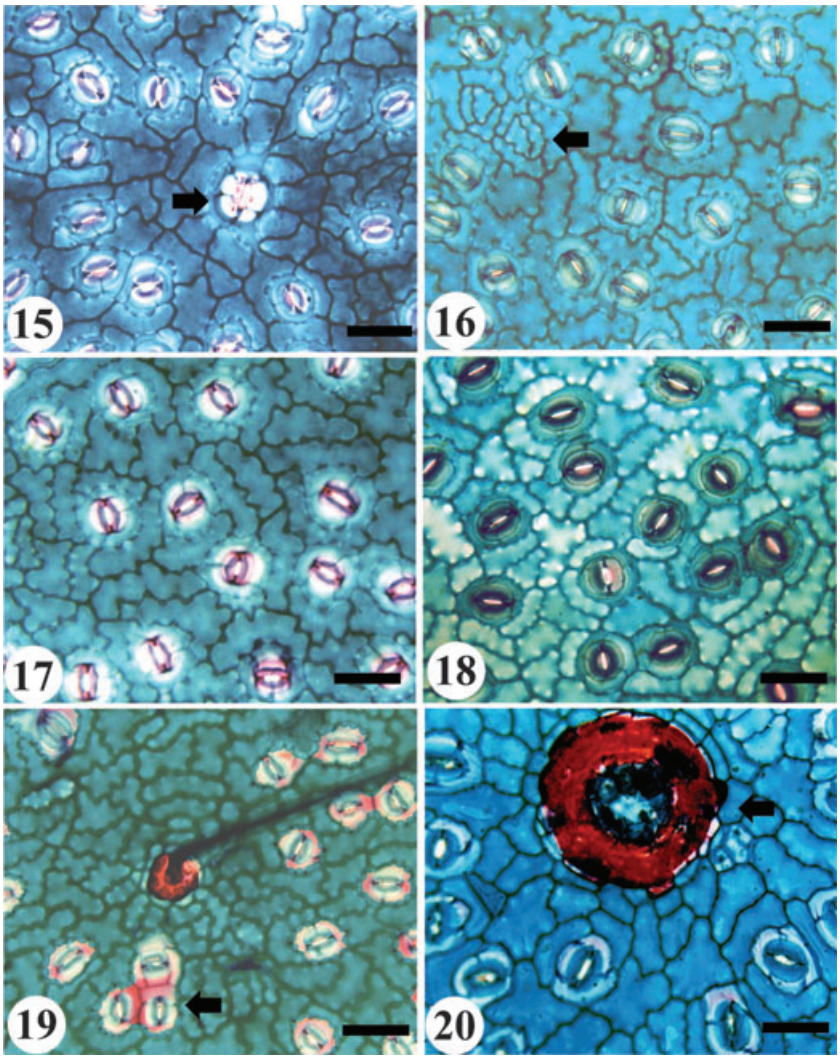


Figures 9–14. The characters of the abaxial epidermis under the light microscope. Figures 9, 10. The anticlinal walls of abaxial epidermal cells. Fig. 9. *C. lanosituba*: sinuous. Fig. 10. *C. trichosperma*: repand. Figures 11–14. Showing two distinct types of stomatal apparatus within the same species. One is centre stomata (arrows). The other is anisocytic stomata. Fig. 11. *C. brevipetiolata*. Fig. 12. *C. lungshenensis*. Fig. 13. *C. cryptoneura*. Fig. 14. *C. brevicolumna*. Scale bar, 50 μm.

Table 4. The area, perimeter, length and width of the guard cell of centre stomata and common stomata in two species

Taxa	Stoma types	Area (μm^2)	Perimeter (μm)	Length (μm)	Width (μm)
C. lungshenensis	Centre stomata (cyclocytic)	556.26 ± 55.48†	63.74 ± 3.58†	31.48 ± 2.97†	15.56 ± 2.39†
	Common stomata (anisocytic)	387.48 ± 28.03‡	53.46 ± 2.47‡	28.36 ± 1.74‡	13.90 ± 0.84‡
C. cryptoneura	Centre stomata (cyclocytic)	666.34 ± 95.75†	72.78 ± 4.10†	36.08 ± 2.69†	15.54 ± 1.34†
	Common stomata (anisocytic)	431.30 ± 18.74‡	59.86 ± 2.86‡	28.40 ± 2.41‡	13.08 ± 0.96‡

Note: Duncan's Multiple Range Test is made by the SAS program (version 9.0).
†, ‡Means with the same symbol are not significantly different ($P = 0.05$).



Figures 15–20. The characters of the abaxial epidermis under the light microscope. Fig. 15. *C. xifongensis*: non-clustered stomata and abortive stomata (arrow). Fig. 16. *C. brachygyna*: single-distributed stomata. Figs 17, 18. Showing stomatal clusters: 2–4 stomata arranged adjacently. Fig. 17. *C. bambusifolia*: stomatal clusters with two stomata arranged adjacently. Fig. 18. *C. delicate*: showing stomatal clusters (arrow) and hairs. Fig. 19. *C. phellocapsa*: showing anisocytic stomata (arrowhead) and stomatal cluster (arrow). Fig. 20. *C. compressa*: showing cork wart (arrow). Scale bar, 50 μm.

Stone cells (Fig. 34) and crystals are randomly present in the veins of all species examined.

PCA Based on measurements of leaf morphology

The average values of lamina vertical length, horizontal width, ratio of width and length (W/L), area and leaf veins (Table 6, Supplementary, Appendix S1) were transformed before they were used for PCA. The PCA results (Fig. 35) indicate that component 1 and component 2 account for 63.2 and 20.6% of the total variance, respectively. Thus, the sum of the two components accounts for most of the total variance. In Figure 35, to compare readily the treatments of Chang (1998) and Ming (2000), we use the number codes (Table 3) to represent species or varieties in Chang's treatment and tag them with corresponding symbols indicating their taxonomic status in Ming's treatment. The scatter diagram (Fig. 35) shows that *C. trichosperma*, *C. semiserrata*, *C. semiserrata* var. *albiflora* and *C. magnocarpa* cluster together. It also indicates that *C. compressa*, *C. paucipetala*, *C. changii*, *C. crassissima* and *C. apolyodonta* have particular leaf morphology and are thus distinct from other species.

Cluster analysis

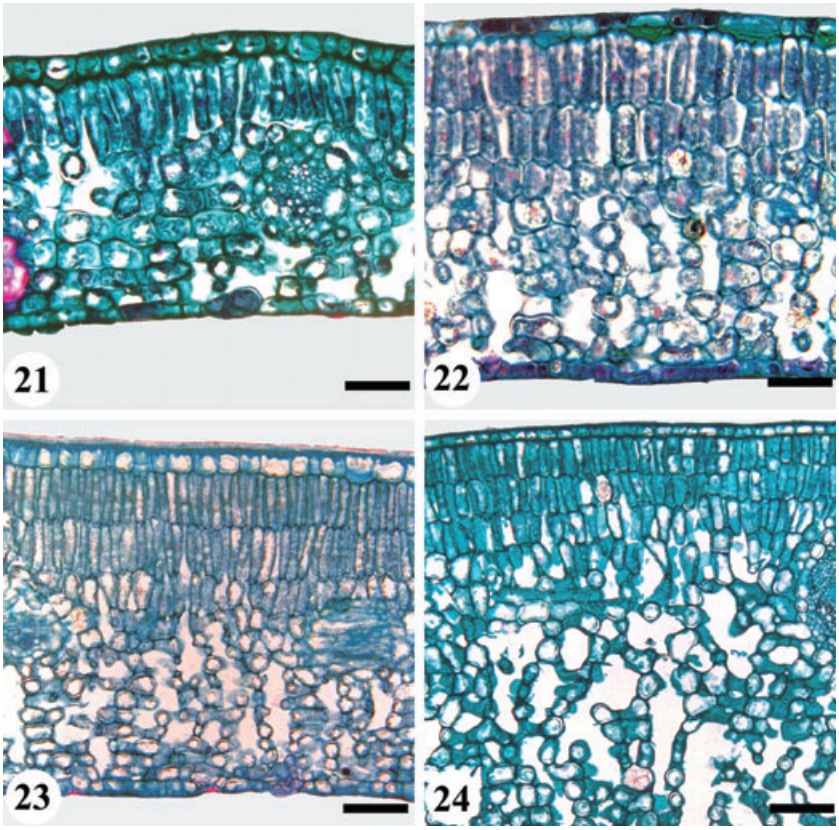
In the cluster analysis, section *Camellia* was divided into two main clusters: cluster 1 (C1) consisting of

Table 5. Characters in transverse section

Taxa	Upper epidermis		Lower epidermis	Mesophyll			
				Palisade tissue			Spongy tissue
	Thickness (μm)*	Multiple epidermis	Thickness (μm)*	Stone cells	Thickness (μm)*	Layers	Thickness (μm)*
C. jinshajiangica	26.37 ± 4.22	Absent	25.98 ± 3.13	Present	128.8 ± 7.01	2	247.1 ± 18.30
C. omeiensis	37.33 ± 3.06	Absent	19.18 ± 1.74	Present	161.3 ± 4.81	2	207.5 ± 8.24
C. polyodonta	12.62 ± 0.71	Discontinuous	13.39 ± 1.87	Present	92.57 ± 4.39	2	167.8 ± 4.28
C. lanosituba	15.95 ± 2.80	Absent	15.84 ± 1.23	Present	91.04 ± 4.00	2	170.8 ± 6.29
C. longigyna	22.22 ± 3.83	Absent	14.35 ± 2.75	Present	50.08 ± 4.55	1	119 ± 8.35
C. lapidea	24.04 ± 2.14	Discontinuous	15.48 ± 0.93	Present	114 ± 4.97	2	186.2 ± 3.79
C. phelloderma	26.96 ± 2.96	Discontinuous	15.12 ± 1.85	Present	100.7 ± 7.07	2	184.6 ± 13.90
C. mairei	19.53 ± 1.58	Discontinuous	16.13 ± 2.84	Present	174.3 ± 7.50	3	189.1 ± 3.27
C. villosa	26.61 ± 3.29	Discontinuous	15.93 ± 1.93	Present	126.1 ± 6.47	1	133.7 ± 6.45
C. trichosperma	42.34 ± 3.04	Discontinuous	18.96 ± 2.28	Present	95.79 ± 3.00	2	127.9 ± 4.44
C. semiserrata	46.8 ± 1.13	Discontinuous	23.53 ± 1.67	Present	62.35 ± 3.52	2	172.4 ± 2.71
C. reticulata	24.17 ± 1.83	Absent	20.48 ± 1.76	Present	141.2 ± 22.05	2	174 ± 6.80
C. semiserrata var. *albiflora*	30.78 ± 2.55	Absent	19.41 ± 2.25	Present	128.3 ± 5.86	2	157.1 ± 18.01
C. brevipetiolata	18.39 ± 2.29	Absent	19.29 ± 2.23	Present	159.2 ± 9.73	2	224.4 ± 5.70
C. phellocapsa	18.63 ± 1.68	Absent	13.01 ± 1.36	Present	88.83 ± 6.43	1	95.05 ± 8.35
C. compressa	39.88 ± 4.86	Discontinuous	20.24 ± 2.23	Present	185.6 ± 6.30	2	285.2 ± 7.52
C. magniflora	24.98 ± 1.96	Absent	19.9 ± 2.52	Present	144.5 ± 11.89	2	210.1 ± 8.29
C. lungshenensis	20.72 ± 2.13	Discontinuous	15.3 ± 1.19	Present	137 ± 9.57	2	227.9 ± 14.48
C. brevicolumna	23.04 ± 1.92	Absent	20.17 ± 2.18	Present	131.1 ± 2.73	2	217.8 ± 5.08
C. pitardii	16.26 ± 3.09	Absent	11.92 ± 1.15	Present	106.4 ± 3.67	2	175.5 ± 3.27
C. pitardii var. *alba*	19.62 ± 2.04	Discontinuous	12.15 ± 1.64	Present	145.4 ± 6.20	2	188.2 ± 7.04
C. pitardii var. *yunnanica*	30.14 ± 3.46	Discontinuous	15.8 ± 1.66	Present	155.3 ± 14.58	2	198.7 ± 8.58
C. xifongensis	28.88 ± 2.19	Absent	16.55 ± 1.49	Present	132.1 ± 6.56	2	223.7 ± 16.08
C. hongkongensis	14.98 ± 1.40	Discontinuous	14.94 ± 1.56	Present	84.17 ± 6.35	2	158.6 ± 8.66
C. cryptoneura	15.22 ± 1.46	Absent	20.74 ± 1.85	Present	191.1 ± 6.77	2	208.2 ± 4.25
C. oviformis	18.99 ± 1.89	Absent	20.73 ± 2.34	Present	169.2 ± 4.41	2	184.5 ± 6.74
C. brachygyna	24.36 ± 2.21	Absent	21.81 ± 1.99	Present	148.6 ± 9.72	2	194.1 ± 8.03
C. tunganica	22.03 ± 1.22	Discontinuous	14.18 ± 1.86	Present	159.9 ± 10.62	2	169 ± 10.82
C. bambusifolia	32.56 ± 2.17	Discontinuous	26.17 ± 2.42	Present	84.16 ± 4.99	1	140.1 ± 7.44
C. saluenensis	31.42 ± 3.76	Absent	15.39 ± 2.82	Present	129.3 ± 4.81	3	167.7 ± 7.93

C. albo–sericea	17.92 ± 1.68	Absent	16.31 ± 1.16	Present	132.1 ± 7.12	2	252.1 ± 33.95
C. bailinshanica	8.57 ± 1.75	Absent	7.99 ± 2.36	Present	86.54 ± 3.06	4	151.6 ± 6.95
C. oligophlebia	27.54 ± 1.91	Discontinuous	12.62 ± 2.02	Present	164 ± 13.30	2	212.7 ± 4.96
C. uraku	14.35 ± 1.73	Discontinuous	15.83 ± 1.29	Present	146.9 ± 6.84	3	228.3 ± 5.29
C. edithae	18.89 ± 1.40	Absent	13.33 ± 0.95	Present	113.2 ± 8.14	2	200 ± 16.16
C. paucipetala	25.78 ± 2.10	Discontinuous	13.68 ± 2.04	Present	161.3 ± 6.78	2	184.5 ± 8.45
C. tenuivalvis	17.98 ± 1.54	Absent	14.64 ± 1.58	Present	99.07 ± 6.16	2	165.7 ± 3.46
C. boreali–yunnanica	28.61 ± 1.43	Absent	20.19 ± 1.81	Present	169.2 ± 16.77	2	182 ± 11.47
C. hilisciflora	24.72 ± 2.35	Discontinuous	18.69 ± 0.69	Present	120.9 ± 5.42	2	150.5 ± 9.60
C. concina	21.79 ± 1.69	Absent	18.28 ± 1.61	Present	153 ± 4.60	3	133.1 ± 5.04
C. glabsipetala	24.47 ± 2.42	Absent	18.63 ± 1.21	Present	150.8 ± 4.88	2	223.4 ± 4.03
C. delicata	18.04 ± 0.98	Discontinuous	18.66 ± 2.52	Present	72.64 ± 5.29	1	184.3 ± 18.04
C. hunanica	21.02 ± 3.45	Discontinuous	14.47 ± 1.35	Present	131.3 ± 14.52	2	178 ± 4.76
C. glabriperulata	19.41 ± 2.05	Absent	19.29 ± 2.14	Present	112.9 ± 5.64	2	164 ± 8.40
C. magnocarpa	26.33 ± 3.47	Discontinuous	16.37 ± 1.67	Present	50.9 ± 3.07	2	165.3 ± 8.17
C. liberistamina	35.32 ± 2.75	Discontinuous	23.17 ± 1.39	Present	184.4 ± 17.31	2	260.2 ± 6.51
C. lucidissima	33.5 ± 2.82	Absent	19.68 ± 1.88	Present	149.5 ± 14.80	2	241.8 ± 7.22
C. chekiangoleosa	24.55 ± 1.90	Absent	18.6 ± 1.99	Present	183.7 ± 8.84	3	352.1 ± 10.94
C. mongshanica	35.26 ± 4.63	Discontinuous	16.59 ± 1.45	Present	107 ± 2.69	2	200.6 ± 5.67
C. japonica var. *japonica*	20.4 ± 3.55	Discontinuous	13.1 ± 1.43	Present	93.41 ± 5.45	2	275.6 ± 4.71
C. japonica subsp. *rusticana*	26.51 ± 2.22	Continuous	13.73 ± 1.11	Present	75.39 ± 2.64	2	176.7 ± 5.92
C. azalea	32.58 ± 1.82	Discontinuous	25.21 ± 3.01	Absent	70.72 ± 3.58	1	222.3 ± 6.08
C. subintegra	22.99 ± 3.09	Discontinuous	15.36 ± 1.77	Present	166.7 ± 4.85	3	227.7 ± 6.39
C. lienshanensis	39.84 ± 2.07	Absent	22.39 ± 1.58	Present	120.2 ± 4.91	2	214 ± 8.89
C. crassissima	37.23 ± 3.16	Absent	22.33 ± 4.01	Present	174.9 ± 17.06	3	264.4 ± 12.59
C. apolyodonta	18.42 ± 1.48	Discontinuous	13.63 ± 2.29	Present	97.16 ± 6.22	2	125.2 ± 7.34
C. longicaudata	25.67 ± 2.69	Absent	22.23 ± 2.24	Present	157.6 ± 7.47	2	298.1 ± 9.19

*Thickness (±SD) is the average value of 10 measurements.



Figures 21–24. Showing the number of layers of palisade cells. Fig. 21. *C. longigyna*: one layer of palisade cells. Fig. 22. *C. hongkongensis*: two layers of palisade cells. Fig. 23. *C. crassissima*: three layers of palisade cells. Fig. 24. *C. bailinshanica*: four layers of palisade cells. Scale bar, 50 μm.

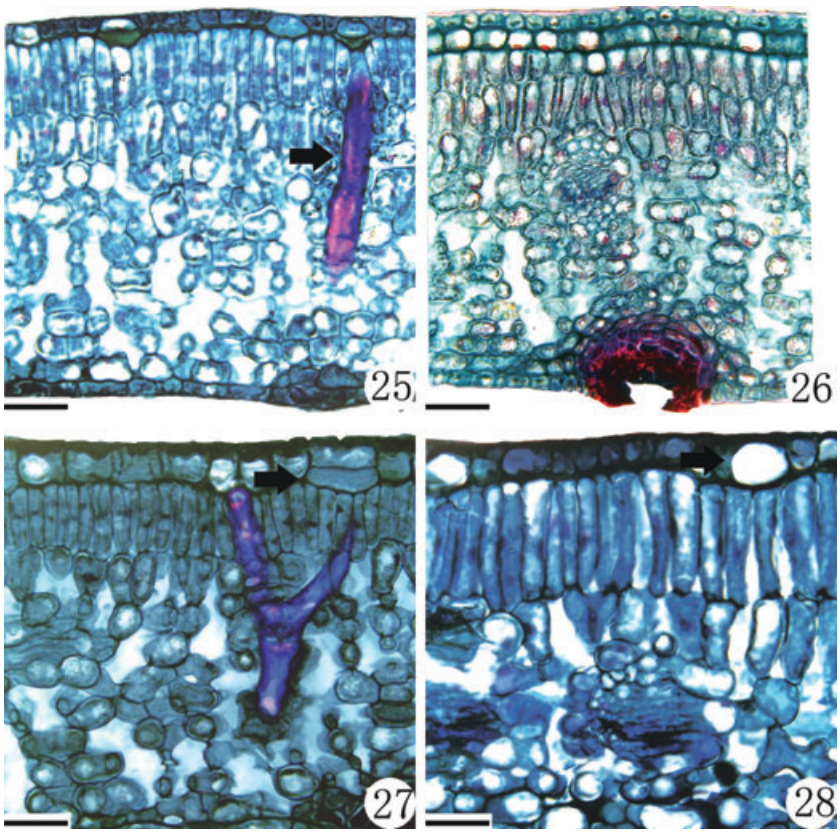
only one species, *C. edithae*; and cluster 2 (C2) including the remaining species (Fig. 36). On closer inspection, C2 can be seen to contain two subclusters: subcluster 1 (SC1) comprising the 12 species and one variety with centre stomata; subcluster 2 (SC2) containing the remaining 39 species, one subspecies and three varieties. Six groups have similarity values greater than 0.96. These groups are: (1) *C. japonica* and *C. rusticana*; (2) *C. pitardii*, *C. pitardii* var. *yunnanica* and *C. pitardii* var. *alba*; (3) *C. trichosperma*, *C. semiserrata*, *C. semiserrata* var. *albiflora* and *C. magnocarpa*; (4) *C. tunganica* and *C. hunanica*; (5) *C. crassissima* and *C. mongshanica*; and (6) *C. albo-sericea* and *C. bailinshanica*.

DISCUSSION

Stomata of section *Camellia*

Of the epidermal features, stomatal characters are the most important in taxonomy and classification because they are not only easily observed but also constant within the same taxon. Previous works (Solereder, 1908; Keng, 1962; Ao *et al.*, 2002; Yang *et al.*, 2003) have described stomatal patterns in the genus *Camellia*, subfamily Theoideae and family Theaceae. However, their studies are not consistent with our investigations of section *Camellia* in the genus *Camellia*.

Solereder (1908) first studied the patterns of stomatal apparatus of three species of Theaceae, proposing that there are two types of stomatal apparatus in this family. In one type, the guard cells (GCs) are surrounded by the subsidiary cells that are not distinguishable from the common epidermal cells. In the other type, the guard cells are usually surrounded by three (rarely two or four) narrow but distinguishable subsidiary cells. Keng (1962) defined the latter as the gordoniaceous type and suggested that this type was transitional between the anomocytic type (no distinguishable subsidiary cells surrounding guard cells) and the paracytic type (with two subsidiary cells surrounding and parallel to the guard cells). Having observed the stomata of Theaceae, he reported that all species in subfamily Theoideae share the gordoniaceous type, with the exception of the genus *Pyrenaria*. However, Yang *et al.* (2003) reported that all genera, including *Pyrenaria*, share the gordoniaceous type. He considered that the intermediate type between the



Figures 25–28. Characters of transverse view. Fig. 25. *C. polyodonta*: showing stone cells (arrow). Fig. 26. *C. japonica* and *C. rusticana*: showing continuous multiple eidermis in the adaxial epidermis. Fig. 27. *C. magnocarpa*: showing discontinuous multiple eidermis (arrow). Fig. 28. *C. boreali-yunnanica*: large epidermal cells (arrow), containing few contents. Scale bar, 50 μm.

anomocytic type and paracytic types more exactly matched the anisocytic type. Ao *et al.* (2002, 2007) pointed out that all of *Camellia* spp. share the cyclocytic type.

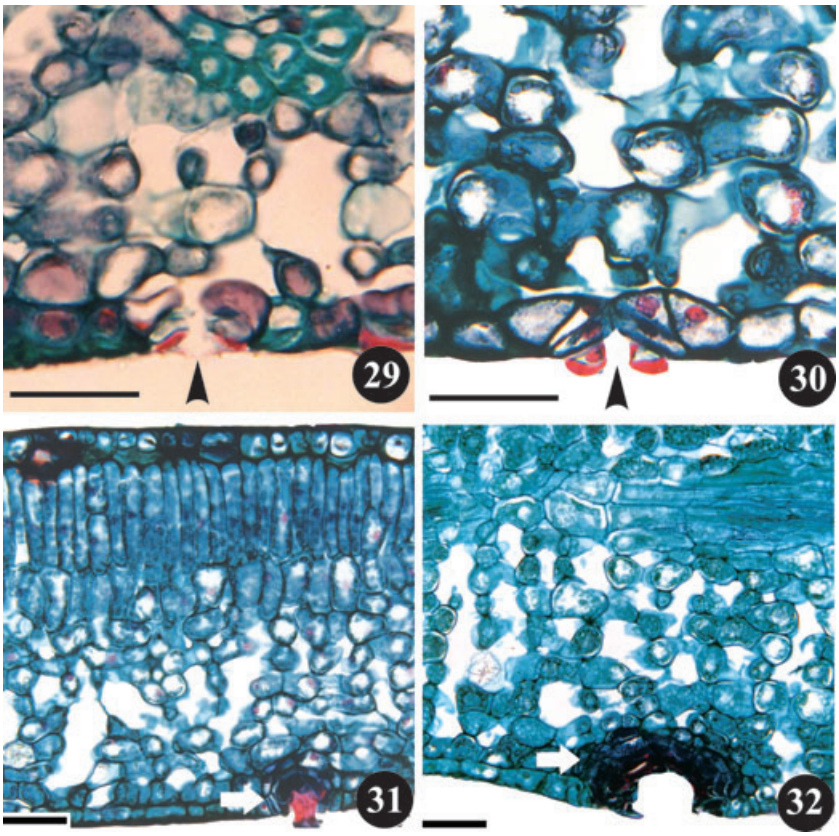
Our investigations reveal that, in section *Camellia*, some species have two distinct types of stomata (one strikingly large, surrounded by four or more subsidiary cells, and the other smaller, surrounded by three subsidiary cells that are more frequently variable in size), whereas most of species share one type. Some species have particularly large cyclocytic stomata that are situated at the centre of a few markedly smaller anisocytic stomata arranged in the form of ring. We define the large cyclocytic stoma as the centre stomata for its position. Large cyclocytic stomata and centre stomata are significant for classification and identification.

Stomatal clusters (Yang & Sack, 1995; Geisler *et al.*, 1998; Tang *et al.*, 2002) or stomata in groups (Metcalfe & Chalk, 1979) have only rarely been reported in *Camellia*. Our examinations show that stomatal clusters are composed of 2–4 adjacent stomata with common subsidiary cells. Most species examined have stomatal clusters which are readily discriminated under LM and are useful in taxonomy.

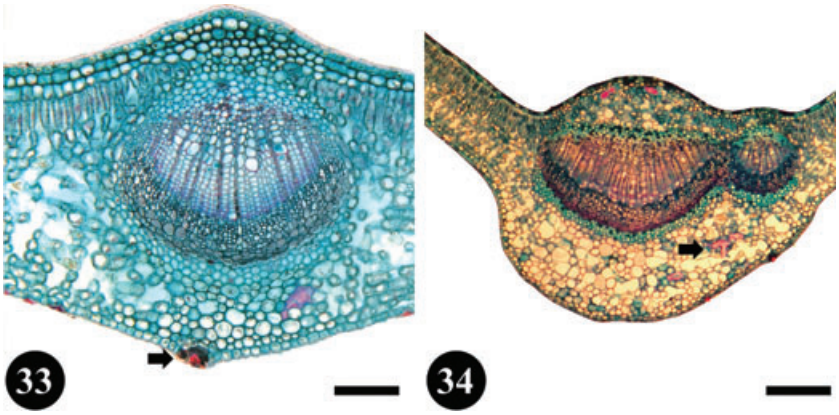
In the transverse section, the guard cell pairs can be seem to lie on, rather than be parallel to, the subsidiary cells. Therefore, in the surface view, most subsidiary cells are covered by guard cells and the subsidiary cells frequently appear narrow or even invisible. This may be the reason that Solereder (1908) noted that one type of stomatal apparatus lacked subsidiary cells and the other type had narrow ones.

Reconsideration of taxonomic treatments in section *Camellia*

At present, Chang's and Ming's taxonomic treatments are the two well-known taxonomic treatments of *Camellia*, but there are many differences between them. Chang's treatment, revised three times (Chang, 1981; Chang & Bartholomew, 1984; Chang, 1998), suggested that *Camellia* consisted of four subgenera, 22 sections and *c.* 280 species. Ming following Sealy (1958), proposed that *Camellia* included two subgen-



Figures 29–32. Characters of transverse section view. Fig. 29. *C. boreali-yunnanica*: showing common stomata in transverse view. Guard cells lying on a single subsidiary cell (white arrow). Fig. 30. *C. brevipetiolata*: Showing especial stomata with guard cells lying on two superposed subsidiary cells. Fig. 31. *C. villosa*: showing hairs' transection view. Fig. 32. *C. oligophlebia*: showing cork wart's transverse section view. Scale bar, 50 μm.



Figures 33–34. Characters of veins in the transverse view. Fig. 33. *C. japonica* and *C. rusticana*: showing cork wart (arrow) on the veins. Scale bar, 100 μm. Fig. 34. *C. hongkongensis*: showing stone cells in the veins (arrow). Scale bar, 250 μm.

era, 14 sections and 119 species. Chang (1998) suggested that section *Camellia* contained *c*. 60 species, whereas Ming (1998) treated many species as subspecies or synonyms and reduced it to 12 species and six varieties. These differences are shown in Figure 37.

With the exception of *C. hongkongensis*, *C. changii* and *C. edithae*, all the species in section *Camellia* were more or less merged by Ming (2000) (Fig. 37). Additionally, *C. uraku* was treated as a hybrid of *C. japonica* in Ming's treatment. Results show that

Table 6. The mean values of leaf area (cm^2), perimeter (cm), vertical length (cm), horizontal width (cm), the ratio of width and length (W/L) and form coefficient, with values representing character states of leaf veins (1, not raised; 2, slightly raised; 3, raised)

No.	Taxa	Area	Perimeter	Vertical length	Horizontal width	W/L	Form cofficient	Veins
1	*C. jinshajiangica*	27.93 ± 2.31	24.66 ± 2.72	8.36 ± 0.56	4.92 ± 0.23	0.59 ± 0.03	0.59 ± 0.09	1
2	*C. omeiensis*	29.25 ± 1.91	28.30 ± 1.10	10.90 ± 0.84	4.30 ± 0.23	0.40 ± 0.05	0.46 ± 0.01	3
3	*C. polyodonta*	44.45 ± 1.52	30.39 ± 4.84	11.32 ± 0.30	5.66 ± 0.22	0.50 ± 0.01	0.62 ± 0.18	3
4	*C. lanosituba*	27.58 ± 2.99	25.81 ± 1.69	10.22 ± 0.85	4.18 ± 0.20	0.41 ± 0.02	0.52 ± 0.02	1
5	*C. longigyna*	21.30 ± 0.57	27.50 ± 0.56	10.34 ± 0.27	3.20 ± 0.08	0.31 ± 0.00	0.35 ± 0.01	3
6	*C. lapidea*	18.46 ± 0.81	23.66 ± 1.16	7.88 ± 0.46	3.50 ± 0.11	0.44 ± 0.02	0.42 ± 0.02	3
7	*C. phelloderma*	21.33 ± 2.58	25.98 ± 1.17	8.95 ± 0.41	3.77 ± 0.22	0.42 ± 0.02	0.40 ± 0.03	2
8	*C. mairei*	25.06 ± 2.19	26.46 ± 1.45	10.39 ± 0.62	3.74 ± 0.22	0.36 ± 0.02	0.45 ± 0.01	3
9	*C. villosa*	20.65 ± 2.55	26.41 ± 1.46	8.96 ± 0.59	3.61 ± 0.25	0.40 ± 0.02	0.37 ± 0.03	3
10	*C. trichosperma*	69.57 ± 3.72	34.32 ± 0.36	11.45 ± 0.02	7.96 ± 0.22	0.70 ± 0.02	0.74 ± 0.02	1
11	*C. semiserrata*	69.56 ± 2.63	34.32 ± 0.26	11.45 ± 0.02	7.96 ± 0.15	0.70 ± 0.01	0.74 ± 0.02	1
12	*C. reticulata*	29.90 ± 5.19	25.61 ± 2.29	9.82 ± 0.64	4.29 ± 0.47	0.44 ± 0.03	0.57 ± 0.04	2
13	*C. semiserrata* var. *albiflora*	69.57 ± 2.63	34.32 ± 0.26	11.45 ± 0.02	7.96 ± 0.15	0.70 ± 0.01	0.74 ± 0.02	1
14	*C. brevipetiolata*	32.63 ± 1.71	29.42 ± 1.35	10.07 ± 0.30	4.67 ± 0.25	0.46 ± 0.03	0.47 ± 0.02	1
15	*C. phellocapsa*	25.79 ± 2.00	24.29 ± 1.21	9.13 ± 0.47	4.12 ± 0.23	0.45 ± 0.03	0.55 ± 0.02	3
16	*C. compressa*	58.77 ± 4.55	42.30 ± 2.19	15.41 ± 0.55	5.72 ± 0.31	0.37 ± 0.01	0.41 ± 0.02	2
17	*C. magniflora*	46.42 ± 6.24	33.85 ± 1.98	11.62 ± 0.67	5.81 ± 0.46	0.50 ± 0.02	0.51 ± 0.04	1
18	*C. lungshenensis*	42.06 ± 4.91	32.09 ± 1.06	11.07 ± 0.48	5.52 ± 0.45	0.50 ± 0.02	0.51 ± 0.03	2
19	*C. brevicolumna*	26.72 ± 1.18	30.38 ± 1.10	9.20 ± 0.36	4.54 ± 0.15	0.49 ± 0.03	0.36 ± 0.01	1
20	*C. pitardii*	16.28 ± 1.29	23.42 ± 0.72	8.39 ± 0.36	3.02 ± 0.15	0.36 ± 0.02	0.37 ± 0.03	2
21	*C. pitardii* var. *alba*	13.46 ± 0.86	19.64 ± 0.96	7.19 ± 0.36	2.93 ± 0.14	0.41 ± 0.02	0.44 ± 0.03	2
22	*C. pitardii* var. *yunnanica*	17.40 ± 0.71	23.94 ± 0.59	8.23 ± 0.28	3.26 ± 0.15	0.40 ± 0.02	0.38 ± 0.02	2
23	*C. xifongensis*	26.93 ± 2.32	31.99 ± 2.08	11.02 ± 0.56	3.84 ± 0.24	0.35 ± 0.02	0.33 ± 0.02	2
24	*C. hongkongensis*	23.00 ± 2.41	30.49 ± 2.68	9.96 ± 0.75	3.69 ± 0.12	0.37 ± 0.02	0.31 ± 0.02	2
25	*C. cryptoneura*	36.14 ± 2.07	31.33 ± 0.79	11.14 ± 0.38	4.91 ± 0.15	0.44 ± 0.03	0.46 ± 0.04	2
26	*C. oviformis*	33.01 ± 3.01	26.70 ± 0.78	9.18 ± 0.56	5.31 ± 0.22	0.58 ± 0.05	0.58 ± 0.04	2
27	*C. brachygyna*	24.65 ± 1.63	25.35 ± 0.98	9.92 ± 0.37	3.93 ± 0.23	0.40 ± 0.03	0.48 ± 0.02	2
28	*C. tunganica*	22.13 ± 1.01	23.32 ± 0.82	8.61 ± 0.30	3.71 ± 0.09	0.43 ± 0.02	0.51 ± 0.03	2
29	*C. bambusifolia*	10.25 ± 1.56	17.46 ± 0.89	6.65 ± 0.55	2.28 ± 0.16	0.34 ± 0.01	0.42 ± 0.02	2

Table 6. *Continued*

No.	Taxa	Area	Perimeter	Vertical length	Horizontal width	W/L	Form cofficient	Veins
30	*C. saluensis*	8.25 ± 1.73	15.85 ± 1.65	5.92 ± 0.61	2.05 ± 0.23	0.35 ± 0.00	0.41 ± 0.01	2
31	*C. albo–sericea*	21.86 ± 1.66	23.62 ± 0.61	9.04 ± 0.32	3.75 ± 0.18	0.41 ± 0.01	0.49 ± 0.03	2
32	*C. bailinshanica*	20.30 ± 1.10	26.19 ± 0.74	9.44 ± 0.23	3.37 ± 0.21	0.36 ± 0.02	0.37 ± 0.02	2
33	*C. oligophlebia*	22.69 ± 2.12	22.89 ± 1.32	8.57 ± 0.38	4.13 ± 0.20	0.48 ± 0.01	0.54 ± 0.02	2
34	*C. uraku*	24.59 ± 1.71	23.41 ± 0.99	9.17 ± 0.43	4.09 ± 0.04	0.45 ± 0.02	0.56 ± 0.01	2
35	*C. edithae*	34.15 ± 5.29	27.09 ± 1.74	9.72 ± 0.29	5.03 ± 0.65	0.52 ± 0.05	0.58 ± 0.02	3
36	*C. paucipetala*	8.42 ± 1.03	14.19 ± 1.25	4.68 ± 0.30	2.58 ± 0.14	0.55 ± 0.02	0.53 ± 0.04	1
37	*C. tenuivalvis*	12.24 ± 1.90	16.58 ± 1.36	6.53 ± 0.47	2.77 ± 0.28	0.42 ± 0.02	0.56 ± 0.01	2
38	*C. boreali–yunnanica*	27.70 ± 4.93	27.36 ± 2.80	10.74 ± 1.62	3.92 ± 0.15	0.37 ± 0.04	0.46 ± 0.02	2
39	*C. hilisciflora*	22.59 ± 1.68	27.36 ± 1.04	9.73 ± 0.34	3.76 ± 0.14	0.39 ± 0.01	0.38 ± 0.03	1
40	*C. concina*	7.72 ± 1.13	16.53 ± 1.08	6.03 ± 0.32	2.06 ± 0.23	0.34 ± 0.02	0.35 ± 0.01	2
41	*C. glabsipetala*	9.78 ± 0.78	16.18 ± 0.67	6.31 ± 0.21	2.30 ± 0.14	0.36 ± 0.02	0.47 ± 0.01	2
42	*C. delicata*	13.67 ± 1.67	20.50 ± 1.29	7.30 ± 0.32	3.01 ± 0.24	0.41 ± 0.02	0.41 ± 0.03	3
43	*C. hunanica*	17.44 ± 0.95	20.57 ± 0.78	7.09 ± 0.25	3.58 ± 0.12	0.51 ± 0.01	0.52 ± 0.03	2
44	*C. glabriperulata*	10.69 ± 1.03	15.45 ± 0.87	6.18 ± 0.36	2.48 ± 0.15	0.40 ± 0.03	0.56 ± 0.03	2
45	*C. magnocarpa*	68.55 ± 2.96	34.17 ± 0.36	11.43 ± 0.04	7.87 ± 0.22	0.69 ± 0.02	0.74 ± 0.02	1
46	*C. liberistamina*	31.64 ± 4.99	30.41 ± 2.59	10.78 ± 1.38	4.61 ± 0.46	0.43 ± 0.01	0.43 ± 0.01	1
47	*C. lucidissima*	43.21 ± 0.30	30.99 ± 2.11	11.43 ± 0.62	5.95 ± 0.24	0.52 ± 0.05	0.57 ± 0.07	2
48	*C. chekiangoleosa*	28.27 ± 6.33	25.11 ± 3.55	9.28 ± 1.19	4.55 ± 0.65	0.49 ± 0.04	0.56 ± 0.03	1
49	*C. mongshanica*	31.84 ± 5.09	27.53 ± 3.09	10.03 ± 0.69	4.96 ± 0.72	0.49 ± 0.04	0.53 ± 0.04	2
50	*C. japonica*	17.59 ± 1.22	18.38 ± 0.64	7.13 ± 0.26	3.83 ± 0.24	0.54 ± 0.04	0.65 ± 0.03	2
51	*C. rusticana*	20.08 ± 2.21	20.94 ± 0.62	7.55 ± 0.17	4.05 ± 0.36	0.54 ± 0.04	0.57 ± 0.03	2
52	*C. azalea*	5.62 ± 0.52	11.04 ± 0.65	4.68 ± 0.34	1.70 ± 0.09	0.36 ± 0.03	0.58 ± 0.03	1
53	*C. subintegra*	17.04 ± 3.19	21.80 ± 1.82	9.31 ± 0.89	2.87 ± 0.31	0.31 ± 0.02	0.45 ± 0.02	1
54	*C. lienshanensis*	20.58 ± 1.46	22.11 ± 1.42	8.28 ± 0.58	3.97 ± 0.15	0.48 ± 0.03	0.53 ± 0.05	1
55	*C. crassissima*	1.46 ± 1.46	1.37 ± 1.37	0.95 ± 0.95	0.04 ± 0.04	0.04 ± 0.04	0.03 ± 0.03	2
56	*C. apolyodonta*	37.05 ± 2.43	38.63 ± 0.64	12.17 ± 0.49	4.75 ± 0.15	0.39 ± 0.02	0.31 ± 0.01	3
57	*C. longicaudata*	22.76 ± 1.32	21.82 ± 1.46	10.02 ± 0.43	3.42 ± 0.09	0.34 ± 0.02	0.61 ± 0.11	3

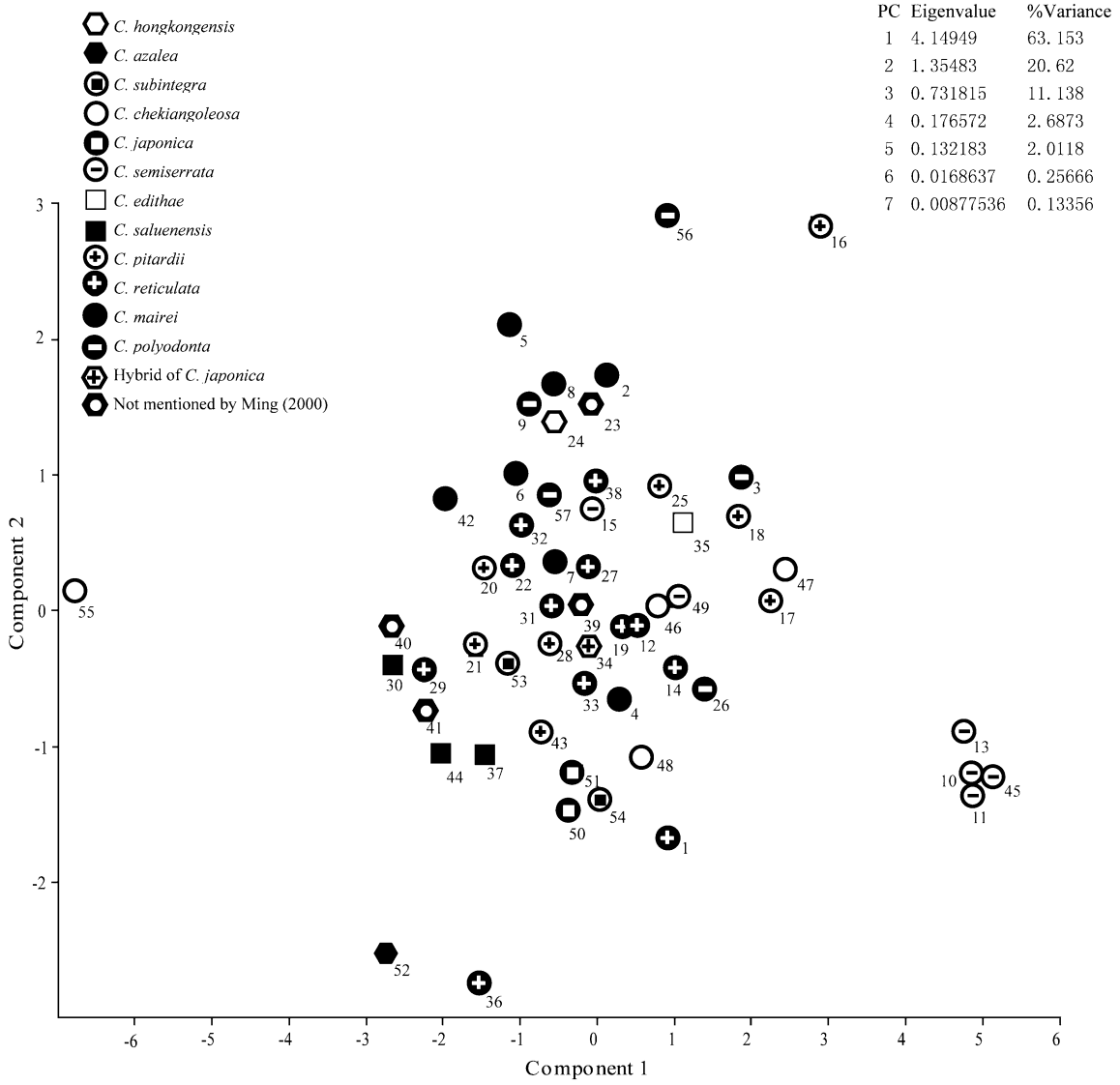


Figure 35. Comparing the taxonomic treatment by Chang (1998) with the treatment by Ming (2000) in *Camellia* section *Camellia*.

C. changii is characterized by its particular leaf shape and the absence of stone cells. *Camellia edithae* differs from the other species by its extremely dense and long hairs. These support the treatment of both Chang (1998) and Ming (2000) of *C. changii* and *C. edithae* as distinctive species, respectively.

Camellia semiserrata, *C. trichosperma*, *C. semiserrata* var. *albiflora* and *C. magnocarpa* share common features, such as centre stomata, straight to curved anticlinal walls of upper epidermal cells, repand anticlinal walls of lower epidermal cells and discontinuous multiple epidermis. Additionally, Figure 36 shows that the leaf morphology of *C. magnocarpa* is similar to that of *C. semiserrata*, *C. trichosperma* and *C. semiserrata* var. *albiflora*. Cluster analysis shows that the similarity value among *C. semiserrata*, *C. trichosperma*, *C. semiserrata* var. *albiflora* and *C. magnocarpa* is larger than 0.96 (Fig. 36). These support the views of Ming (2000) that *C. magnocarpa* is a variety of *C. semiserrata*.

The leaf features of *C. phellocapsa*, including sinuous anticlinal walls of the upper epidermal cells, relatively smaller leaf area and form coefficient, do not agree with the proposal of Ming (2000) to merge *C. phellocapsa* with *C. semiserrata*. This opinion is consistent with that of Gao *et al.* (2005), who claimed that both flower size and foliar serration patterns of *C. phellocapsa* are different from those of *C. semiserrata*. Hence, the taxonomic status of *C. phellocapsa* needs to be reconsidered.

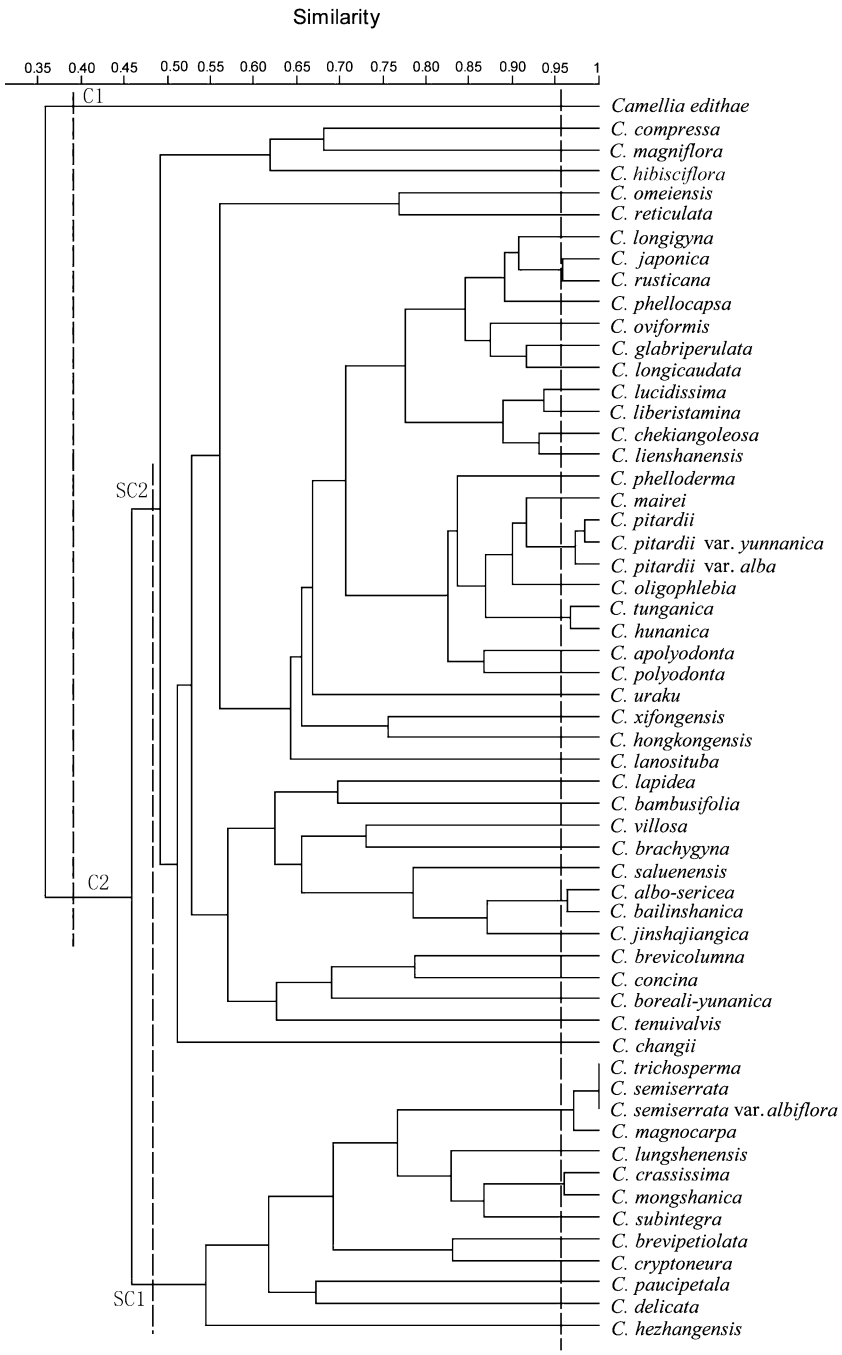


Figure 36. Scatter diagram of principle component analysis (PCA). Axes represent principle components 1 and 2. Each number code (see Table 6) represents a species or variety according to Chang (1998), while corresponding species (displayed in the top left corner) in Ming's (2000) treatment are shown by symbols. The results of PCA are shown in the top right corner.

Chang (1998) noted that all the features of *C. mongshanica* are similar to *C. crassissima*, except that *C. crassissima* had smaller capsules and tomentose seeds. Similar features of leaf morphology and anatomy of *C. mongshanica* and *C. crassissima* seem to support the views of Ming (2000) that *C. mongshanica* should be treated as a variety of *C. semiserrata*. Figure 36 indicates that *C. mongshanica* is a close relative of *C. semiserrata*.

There are few differences between *C. japonica* and *C. rusticana*, except the continuous multiple epidermis in *C. japonica* and the discontinuous multiple

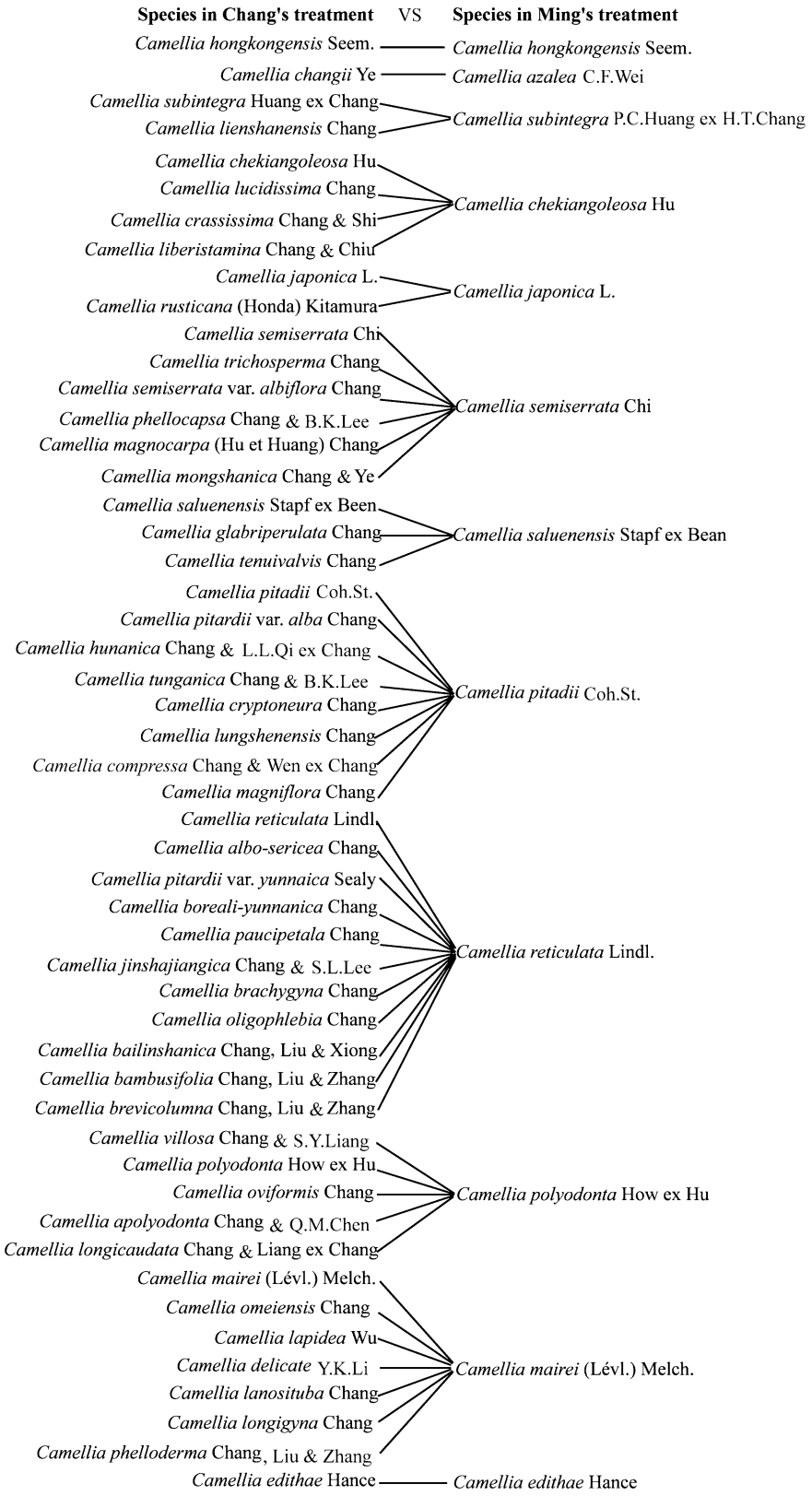


Figure 37. Cluster analysis based on quantitative and qualitative characters.

epidermis in *C. rusticana*. Figure 36 indicates that the leaf morphology of *C. japonica* is similar to that of *C. rusticana*. Our study supports Ming's (2000) treatment of *C. rusticana* as a variety of *C. japonica*.

In the light of Ming's taxonomic treatment, *C. pitardii*, *C. pitardii* var. *alba*, *C. hunanica*, *C. tungannica*, *C. cryptoneura*, *C. lungshenensis*, *C. compressa* and *C. magniflora* are merged into *C. pitardii* and treated as *C. pitardii* var. *pitardii*, *C. pitardii* form. *alba* and *C. pitardii* var. *cryptoneura* (Fig. 37).

It seems unnatural to treat *C. hunanica* and *C. tungannica* as forms of *C. pitardii*. Ming (2000) claimed that *C. hunanica* and *C. tungannica* only differ from *C. pitardii* in white flowers. However, our study reveals that *C. pitardii* differs from *C. hunanica* and *C. tungannica* as follows: (1) both *C. hunanica* and *C. tungannica* have white, fragrant flowers, but *C. pitardii* has red, non-fragrant flowers; (2) both *C. hunanica* and *C. tungannica* have relatively broader leaves, whereas *C. pitardii* has narrow leaves; (3) our cluster analysis demonstrates that the similarity value among *C. pitardii*, *C. hunanica* and *C. tungannica* is rather less than 0.96.

The presence of centre stomata in *C. cryptoneura* and its larger leaf size make it distinct from *C. pitardii*. The chromosome number ($2n = 90$) of *C. cryptoneura* is threefold higher than that of *C. pitardii* ($2n = 30$). The results of PCA (Fig. 35) show that *C. cryptoneura* also differs from *C. pitardii* in leaf morphology. Therefore, we consider there is not enough evidence to merge *C. cryptoneura* into *C. pitardii*. When reconsidering Ming's (2000) merging of *C. compressa* and *C. magniflora* into *C. pitardii*, we also find this unnatural. Examination of anticlinal walls of upper epidermis cells shows that the straight–curved pattern is present in *C. magniflora* and the sinuous pattern in *C. compressa*, whereas *C. pitardii* has the repand pattern. Cork warts are found in *C. compressa* and *C. magniflora*, but not in *C. pitardii*. Ming (2000) noted 'compared to *C. pitardii*, *C. compressa* and *C. magniflora* are distinct due to broader and larger leaf, tip acuminate, serrate (not thinly and sharply serrate), larger flowers and capsules and chromosome number $2n = 90$ or $2n = 120$ (not $2n = 30$).' All these facts indicate that the combination of *C. compressa*, *C. magniflora* and *C. pitardii* needs more evidence. Gao *et al.* (2005) noted 'however, there are significant morphological differences between *C. magniflora* and *C. pitardii*.' We feel the decision to combine these two species should be examined further.

The most extensive combination is that Ming (2000) merged 11 species into *C. reticulata*. We find that *C. albo-sericea* and *C. bailinshanica* share common characters as follows: repand pattern of anticlinal walls of upper epidermal cells, sinuous pattern of anticlinal walls of lower epidermal cells, presence of hairs, centre stomata, presence of stomatal clusters and absence of cork warts. Additionally, their anatomical features are similar: absence of multiple epidermis and presence of stone cells. These pieces of evidence indicate that *C. albo-sericea* is a close relative of *C. bailinshanica*. Figure 36 shows that the similarity value between *C. albo-sericea* and *C. bailinshanica* is larger than 0.96. However, *C. reticulata* is obviously distinct from *C. albo-sericea* and *C. bailinshanica* by varied epidermal cells, straight–curved anticlinal walls of the upper epidermal cells, repand anticlinal walls of the lower epidermal cells and absence of hairs. The comparisons of characters from reproductive organs of *C. albo-sericea*, *C. bailinshanica* and *C. reticulata* are listed as follows (Gao *et al.*, 2005):

1. *C. albo-sericea*: flowers are light red to red, 5–6 cm in diameter, borne at the tip of the shoot and in leaf axils; sepals 8–9, outside surface white–silky pubescent; petals 6–7, 3.0–3.5 cm long, obovate, white–silky pubescent on back, fused with the staminal column from the base up to 5–6 mm; androecium glabrous, *c*. 2 cm, outer layer of stamens fused from the base into a cup to 10 cm long; gynoecium 1.5–2.0 cm long, three styles slightly cleft at the tip, ovary tomentose; capsules globose, 3 locules, pericarp wall 8 mm thick.
2. *C. bailinshanica*: flowers are light red to red, 4–6 cm in diameter, borne at the tip of the shoot and in leaf axils; sepals 7–9, slightly pubescent; petals 6–7, 3.0–4.0 cm long, obovate, white–silky pubescent on back, fused with the staminal column from the base up to 5–6 mm; androecium glabrous, about 2.0–2.5 cm, outer layer of stamens fused from the base into a cup to 5–7 mm long; gynoecium 2.5 cm long, three styles slightly cleft at the tip, ovary tomentose; capsules globose, 3 locules, pericarp wall 1.0 cm thick.
3. *C. reticulata*: flowers are rose–pink, 6.6–10.5 cm in diameter, borne at the tip of the shoot and in leaf axils; perules 7–10, partially persistent, pubescent on both surface; petals 6–9, 5.1–6.8 cm long, obovate or obcordate in shape, cleft at the tip from 4–10 mm, fused with the staminal column from the base up to 15 mm; androecium glabrous, 3.5–3.8 cm long, outer layer of stamens fused from the base into a cup to 2 cm long, approximately 130 stamens; gynoecium 3.7–4.1 cm long, 3–5 mostly glabrous styles, more than one-half fused from the base, ovary tomentose; capsules oblate and indented at the tip, surface rough and scaling, 3–5 locules, pericarp wall 4–8 mm thick.

Therefore, merging *C. albo-sericea* and *C. bailinshanica* into *C. reticulata* should be reconsidered. The

combination of *C. albo-sericea* and *C. bailinshanica* is, however, probably justified.

In summary, section *Camellia* probably contains about 50 species. Although a large volume of data of leaf macromorphology and micromorphology has been obtained in our study, there is still a great deal of work to do because plants have many characters, including those based on morphology, anatomy, chemistry and floral biology. It is not usually considered natural to determine their taxonomic status based on only one or two characters. Our study provides data for leaf anatomical and morphological features that lay the basis for further research.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Significance test for leaf morphological and anatomical characters.

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