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基于 mat R 基因序列分析的山茶科系统关系*

杨俊波[1], 杨世雄[1**], 李德铢[1], 雷立公[1], 池田达哉[2], 吉野熙道[3]
(1 中国科学院昆明植物研究所生物多样性与生物地理学重点实验室, 云南 昆明 650204;
2 近畿中国四国农业研究中心遗传工学研究室, 日本 福山 721-0975;
3 冈山大学农学院实验农场, 日本 冈山 700-8530)

摘要: 通过线粒体 *mat*R 基因序列分析探讨了山茶科的分类学范围和系统演化关系。结果显示, 传统山茶科的两个核心——山茶亚科 (Theoideae 或 Camellioideae) 和厚皮香亚科 (Ternstroemioideae) 不构成姐妹群关系, 山茶亚科是一个支持率很高的单系类群, 厚皮香亚科没有形成单系; 山茶亚科下可区分出 3 个明显的分支, 基部的分支由紫茎属 (*Stewartia*) 和舟柄茶属 (*Hartia*) 组成, 木荷属 (*Schima*)、美洲荷属 (*Franklinia*) 和美国大头茶属 (*Gordonia*) 构成第 2 个分支, 该分支与由山茶属 (*Camellia*)、核果茶属 (*Pyrenaria*)、多瓣核果茶属 (*Parapyrenaria*)、石笔木属 (*Tutcheria*)、大头茶属 (*Polyspora*) 和圆籽荷属 (*Apterspema*) 组成的第 3 个分支互为姐妹群。研究结果很好地支持了 Prince 和 Parks 等学者提出的的狭义山茶科 (仅含山茶亚科) 和狭义大头茶属的概念以及科下 3 个族 (紫茎族 Stewartieae、大头茶族 Gordonieae 和山茶族 Theeae) 的划分。但本研究更为清晰地揭示了科下 3 个族间的系统关系, 即紫茎族是最基部的分支, 山茶族与大头茶族间有更近的亲缘关系。同时, 本文认为, 厚皮香 (亚) 科是否为单系类群值得进一步研究。

关键词: *Mat*R 基因序列; 系统发育; 山茶科
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Phylogenetic Relationships of Theaceae Inferred from Mitochondrial mat R Gene Sequence Data

YANG Jun-Bo[1], YANG Shi-Xiong[1**], LI De-Zhu[1], LEI Li-Gong[1],
IKEDA Tatsuya[2], YOSHNO Hiromichi[3]
(1 *Laboratory of Biodiversity and Biogeography*, *Kunming Institute of Botany*, *Chinese Academy of Sciences*, Kunming 650204, China;
2 *Laboratory of Biotechnology*, *National Agricultural Research Center for Western Region*, *6-11-3-502 Nishifukatsu*,
Fukuyama, Hiroshima 721-0975, Japan; 3 *Research Farm & Laboratory of Plant Cytogenetics*,
Faculty of Agriculture, *Okayama University*, Okayama 700-8530, Japan)

Abstract: The circumscription and phylogenetic relationships of Theaceae was investigated using mitochondrial *mat*R sequences data. Phylogenetic analyses based on the *mat*R data, strongly support a monophyletic Theoideae (or Camellioideae) containing three well-supported lineages (Stewartieae, Gordonieae and Theeae), but do not support the sister relationship of Theoideae and Ternstroemioideae, suggesting a paraphyletic Ternstroemioideae. These results are consistent with some recent authors recognizing Theaceae sensu stricto (s. s.) to the exclusion of Ternstroemioideae, and give further support for the three-tribe classification system of Theaceae s. s. of Prince and Parks in 2001. On the other hand, the *mat*R-based analyses provide a better resolution of the phylogeny within Theaceae s. s., i. e., Stewartieae is the basalmost lineage in Theaceae, and Theeae and Gordonieae are closely related with weak support (bootstrap = 64 %).

Key words: *Mat*R sequences; Phylogeny; Theaceae

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** 通讯作者: Author for correspondence. E-mail: shxyang@mail.kib.ac.cn
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作者简介: 杨俊波 (1970-) 男, 高级工程师, 主要从事植物分子生物学研究。

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Introduction

The delimitation and circumscription of Theaceae has been disputed since the family was established by Don (Sprague 1922). The number of taxa included in Theaceae has varied greatly among different classification systems over the past 100 years (Melchior 1925, 1964; Airy-Shaw 1936; Keng 1962; Dahlgren 1980; Cronquist 1981; Goldberg 1986; Thorne 1992; Takhtajan 1997). For example, Cronquist (1981) included four subfamilies in Theaceae: Theoideae, Ternstroemioideae, Bonnetioideae and Asteropeioideae, while Airy-Shaw (1936), Hutchinson (1969), Rouleau (1981), Goldberg (1986), Thorne (1992); and Takhtajan (1997) advocated that the Theaceae is made up of Theoideae (or Camellioideae) and Ternstroemioideae only. Although different views exist, the inclusion of Theoideae (or Camellioideae) and Ternstroemioideae in the core of the Theaceae has been generally accepted.

Recent studies based on molecular data, however, suggested different hypotheses of phylogenetic relationships of Theaceae. Based on sequences of the chloroplast *rbc*L gene DNA, Morton *et al*. (1996, 1997 a, b) found that subfamilies Theoideae and Ternstroemioideae are each monophyletic, but are not sister clades, suggesting a paraphyletic Theaceae. Later analyses using two or more genes (Savolainen *et al*. 2000; Soltis *et al*. 2000; Anderberg *et al*. 2002) also failed to unite the two subfamilies into a monophyletic lineage. These findings support the recognition of two distinct families sensu stricto, *i. e.*, Theaceae and Ternstroemiaceae. Considering that only two or three taxa were sampled for each subfamily in the above analyses, Prince and Parks (2001) carried out a phylogenetic study of Theaceae using more extensive sampling based on sequences of *mat*K and *rbc*L genes. Their results supported families Theaceae s. s. and Ternstroemiaceae, and further identified three strongly supported lineages in Theaceae s. s. (= Theoideae): Theeae, Cordonieae, and Stewartieae. A recent cladistical study based on morphology still supported a monophyletical Theaceae including Theaceae s. s. and Ternstroemiaceae (Luna and Ochoterena, 2004).

Most published molecular data used to address the phylogeny of Theaceae were from the chloroplast genome. Anderberg *et al*. (2002) introduced two mitochondrial genes (*mat*R and *atp*1) into the phylogenetic analysis of Ericales sensu lato including Theaceae, but only three species were sampled for each subfamilies of Theaceae. *Mat*R is a functional gene encoding a maturase-related protein (Wahleithner *et al*. 1990). Generally, it is useful to reconstruct higher-level phylogeny, such as the relationships of orders, families, or distant genera (Qiu *et al*. 1999; Meng *et al*. 2002). In this study, we therefore employed this gene and sampled more theaceous species to reconstruct the phylogeny of the Theaceae.

Materials and Methods

Plant materials

Twenty taxa were sampled to represent the two subfamilies and seventeen genera of Theaceae. *Pentaphylax* and *Sladenia*, which were placed in Theaceae, and several species of Clethraceae, Symplocaceae, Sarraceniaceae, Sapotaceae, Actinidiaceae and Dilleniaceae, were also included in this study since they have been considered to be closely related to Theaceae (e. g., Melchior, 1925, 1964; Keng, 1962; Cronquist, 1981; Prince and Parks, 2001; Anderberg *et al*. 2002). Two paleoherb species (*Saururus chinensis* and *Zippelia begoniaefolia*, Chase *et al*. 1993) were included in the analyses for rooting purposes. All *mat*R sequences were newly obtained in study except for two that were retrieved from the GenBank. Table 1 lists species used in this study, their voucher and GenBank accession numbers. All voucher specimens were deposited in the Herbarium of Kunming Institute of Botany of the Chinese Academy of Sciences, Kunming, Yunnan, P. R. China (KUN).

DNA extraction, PCR amplification and sequencing

Total DNAs were isolated using the CTAB method (Doyle and Doyle, 1987) from silica-gel-dried or fresh leaves. Polymerase chain reaction (PCR) was conducted to amplify the *mat*R gene in GeneAmp 9600 (PE Applied Biosystems, Foster City, CA, USA) using primers *mat*R 26F (5′GACCGCTNACAGTAGTTCT 3′) and *mat*R 1858R (5′TGCTT GTGGGCYRGGGTGAA 3′). PCR program consisted of the initial denature at 94 ℃ for 4 min and 35 cycles, each of which had 1 min denature at 94 ℃, 1 min annealing at 55 ℃, and 1.5 min extension at 72 ℃. After the cycles there was an additional 7 min extension at 72 ℃. PCR products were separated with 1.5 % agarose TAE gel and purified using Wizard PCR preps DNA Purification System (Promega Madison, WI, USA). Purified PCR products were sequenced using the Dideoxy Chain Termination method (Sanger *et al*. 1997) and an ABI PRISM™ Bigdye Terminator Cycle Sequencing Ready Reaction Kit with AmpliTaq DNA polymerase FS (PE Applied Biosystems, Foster City, CA, USA). Four primers

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including 26F, 1858R, 879F (5′ACTAGTTATCAGGTCAGAGA 3′) and 1002R (5′CACCCACGATTCCCAGTAG T 3′) were used for sequencing. Primers were designed by Mark Chase's Molecular Systematic Lab at the Royal Botanic Gardens (Kew, United Kingdom). All protocols of DNA sequencing followed the manufacture's manual. Sequencing was performed using an ABI310 DNA Sequencing System (PE Applied Biosystems, Foster City, CA, USA).

Alignment and analysis of the sequence data

All *mat*R sequences were aligned using the software Clustal X (Thompson *et al*. 1997) and Mega2b3 (Kumar *et al*. 2000) using default settings. The aligned sequences were analyzed using the program PAUP* (version 4.0, Swofford 1998). Phylogenetic analyses were performed using maximum parsimony, distance and maximum likelihood. In the maximum parsimony analysis, Heuristic search, furthest addition sequence and ACCTRAN character-state optimization were used. Gaps were treated as missing data. Trees were rooted using outgroups. Neighbor-joining tree search was carried out using uncorrected distance ("P") and minimum evolution. In the maximum likelihood analysis, we used the following options: Heuristic search, as-is addition sequence, the HKY85 base substitution model, statistical base frequencies, equal distribution of rates at variable sites and unenforced molecular clock. Starting branch lengths were obtained by using Rogers-Swofford approximation method. Support for individual clades of all three analyses was estimated with the bootstrap option in PAUP using 1000 replicates, and the other settings were the same as in other analyses. . .

Table 1　The sources of plant materials used for *mat*R gene sequencing

Taxa	Voucher	Locality*	GenBank #
THEACEAE-THEOIDEAE			
Apterosperma oblata H. T. Chang	S. X. Yang s. n.	Guangdong, China	AY163755
Camellia henryana Coh. St. var. *trichocarpa* (H. T. Chang) Ming	S. X. Yang 95684	Yunnan, China	AY163729
Camellia yunnanensis (Pitard ex Diels) Coh. St. var. *camellioides* (Hu) Ming	S. X. Yang 93408	Yunnan, China	AY163744
Franklinia alatamaha Marshall	J. B. Yang s. n.	AA, US	AY163731
Gordonia lasianthus Linn.	S. X. Yang 991006	Florida Univ., US	AY163735
Hartia sinensis Dunn	S. X. Yang 98913	Yunnan, China	AY163738
Parapyrenaria multisepala (Merr. et Chun) H. T. Chang	S. X. Yang 97792	Hainan, China	AY163742
Polyspora chrysandra Cowan	S. X. Yang s. n.	Yunnan, China	AY163741
Polyspora tonkinensis Pitard	S. X. Yang 98970	Hunan, China	AY163728
Pyrenaria yunnanensis Kurz	S. X. Yang 97797	Yunnan, China	AY163730
Schima khasiana Dyer	S. X. Yang *et al*. 102	Yunnan, China	AY163740
Stewartia gemmata Chien et Cheng	S. X. Yang 98947	Hunan, China	AY163732
Stewartia serrata Maxim.	S. X. Yang s. n.	Yunnan, China	AY163736
Tutcheria spectabilis Dunn	S. X. Yang 97759	Guangxi, China	AY163743
THEACEAE-TERNSTROEMIOIDEAE			
Adinandra hirta Gagnep.	S. X. Yang 98799	Yunnan, China	AY163739
Anneslea fragrans Wall.	S. X. Yang 94554	Yunnan, China	AY163734
Cleyera pachyphylla Chun et H. T. Chang	S. X. Yang s. n.	Yunnan, China	AY163737
Eurya handle-mazzettii H. T. Chang	S. X. Yang 991013	Yunnan, China	AY163748
Euryodendron excelsum H. T. Chang	S. X. Yang 97774	Guangdong, China	AY163733
Ternstroemia gymnanthera (Wight et Arn.) Beddome	S. X. Yang 991001	Yunnan, China	AY163754
CLETHRACEAE			
Clethra delavayi Franch. var. *yuiana* (S. Y. Hu) C. Y. Wu et L. C. Hu	S. X. Yang *et al*. 146	Yunnan, China	AY163746
PENTAPHYLACACEAE			
Pentaphylax euryoides Gardn. et Champ.	S. X. Yang 97788	Hainan, China	AY163749
SAPOTACEAE			
Eberhardtia tonkinensis Lecte.	S. X. Yang 98909	Yunnan, China	AY163750
SARRACENIACEAE			
Darlingtonia californica Torr.	RBGE19840881*A	RBGE, UK	AY163751
SLADENIACEAE			
Sladenia celastrifolia Kurz	S. X. Yang s. n.	Yunnan, China	AY163752
SYMPLOCACEAE			
Symplocos hookeri C. B. Clarke	S. X. Yang s. n.	Yunnan, China	AY163753
ACTINIDIACEAE			
Actinidia rubricaulis Dunn	S. X. Yang s. n.	Yunnan, China	AY163745
DILLENIACEAE			
Dillenia indica L.	S. X. Yang 97753	Guangxi, China	AY163747
SAURURACEAE			
Saururus chinensis (Lour.) Baill.	From GenBank		AF332106
PIPERACEAE			
Zippelia begoniaefolia Bl.	From GenBank		AF332107

*AA: Arnold Arboretum; RBGE: Royal Botanical Garden Edinburgh

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Results

The alignment of all sequences produced a data matrix of 1730 characters, of which 192 (11.1 %) were variable and 104 (6.0 %) parsimony informative. Uncorrected sequence divergence ranged from 0 to 0.58 % within the Theoideae, from 0 to 0.81 % within the Ternstroemioideae, from 0.75 % to 4.92 % between the Theoideae and the out-groups, and from 0.41 % to 4.92 % between the Ternstroemioideae and the out-groups.

Maximum parsimony (MP) analyses

Fourteen most parsimonious trees of 209 steps were obtained with a consistency index (CI) of 0.9426 and a retention index (RI) of 0.9397. In the strict consensus tree (Fig. 1), *Dillenia indica* and *Actinidia rubricaulis* formed a strongly support clade (A, bootstrap support (bs) = 100 %), which is sister to an unresolved clade (B, bs = 81 %) containing the remaining species. Within B clade, subfamily Theoideae formed a well-supported clade (bs = 88 %), containing three subclades. The first and the basal subclade was the Stewartieae-clade (bs = 91 %), where *Hartia sinensis* was sister to a clade of *Stewartia gemmata*-*St. serrata* (bs = 56 %). The other two subclades were Gordonieae and Theeae, which formed a sister relationship with weak support (bs = 64 %). The Gordonieae-clade was well supported (bs = 85 %) and was a trichotomy formed by *Gordonia*, *Schima* and *Franklinia*. The Theeae-clade was strongly supported (bs = 95 %), and was a polytomy composed of *Camellia*, *Polyspora*,

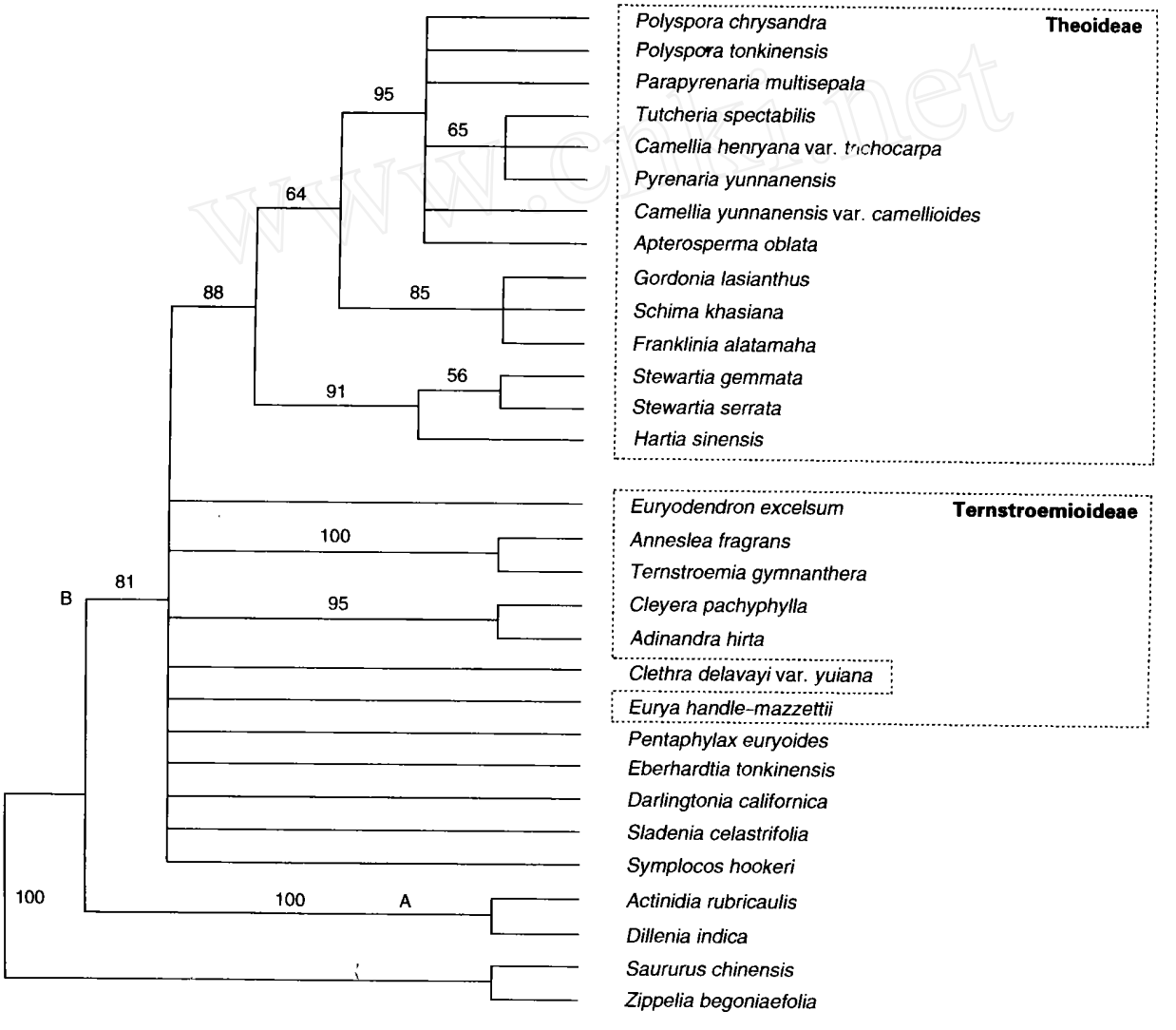

Fig. 1 The strict consensus tree of the 14 most parsimonious trees based on the *mat*R sequences treating gaps as missing data (209 steps, CI = 0.9426, RI = 0.9397). Numbers above the lines represent the bootstrap values in 1000 replicates

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Pyrenaria s. l. (including *Pyrenaria*, *Tutcheria* and *Parapyrenaria*) and *Apterosperma*, in which only *T. spectabilis*, *C. henryana* var. *trichocarpa* and *Pyrenaria yunnanensis* formed a weakly supported trichotomy (bs = 65 %). Subfamilies Ternstroemioideae did not form a clade, and the relationships were not resolved.

Neighbor-joining (NJ) analyses

The neighbor-joining analysis left few taxa in a basal polychotomy (Fig. 2, ME-score = 208.11665). However, most branches had weak bootstrap support (< 50 %), so the NJ tree were essentially identical to the MP tree. Like the MP analysis, Dilleniaceae and Actinidiaceae form a strong clade (bs = 100 %) and is sister (bs = 90 %) to the all other taxa in the ingroups. All taxa of Theoideae are grouped in a clade (bs = 87 %) and display identical topology to the MP tree. The sister-relationship between Theoideae and Ternstroemioideae as well as the monophyly of the later is not supported.

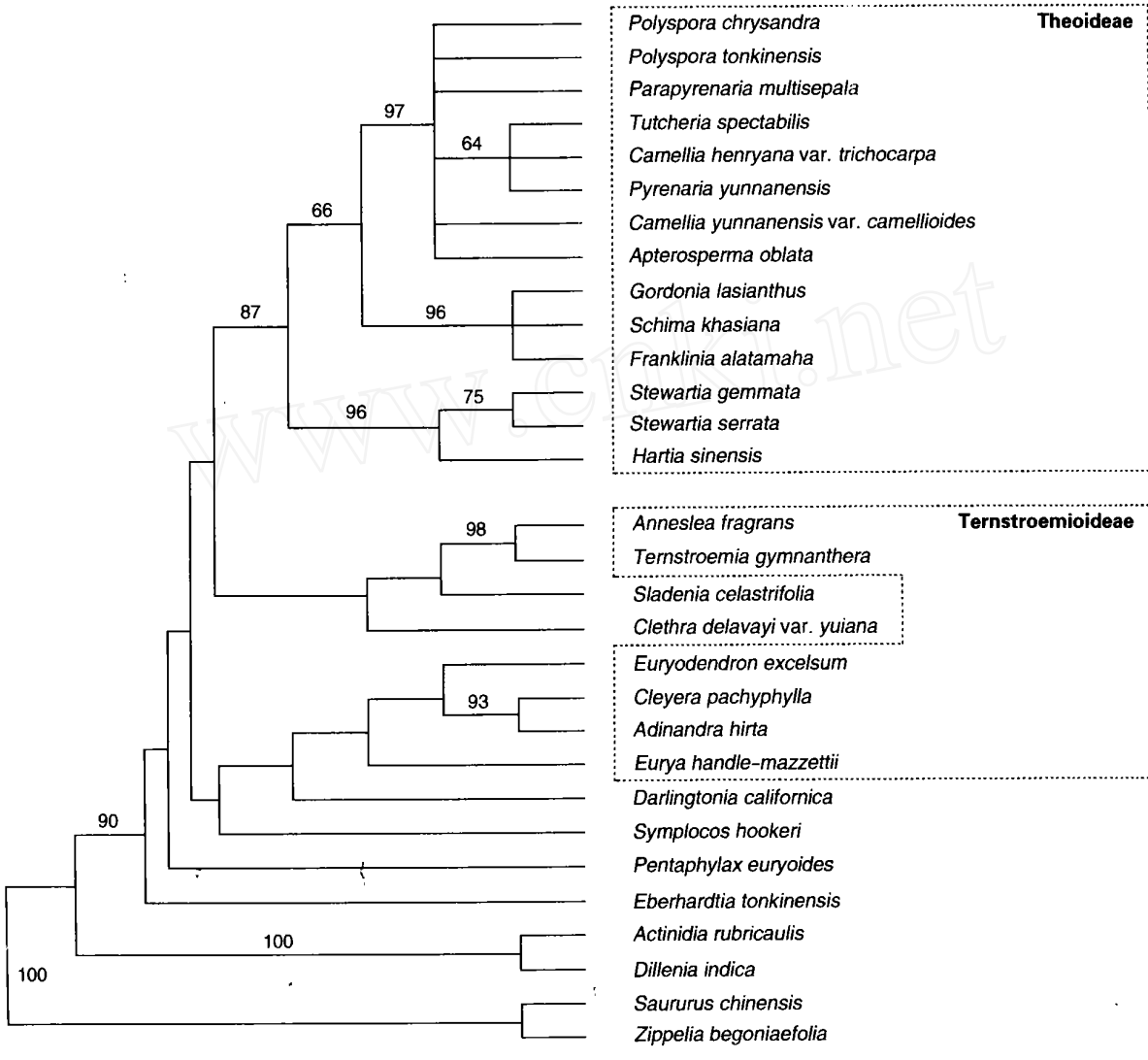

Fig. 2　The neighbor-joining tree obtained based on the *mat*R gene sequences data (ME-score = 208.11665). Numbers above the lines represent the bootstrap values in 1000 replicates

Maximum likelihood (ML) analyses

The maximum likelihood analysis generated a tree and the topology is shown in Fig. 3. (-Ln likelihood = 3836.66389). Again, a monophyletic Theoideae as well as its same topology as MP and NJ analyses was strongly supported. And no evidence supports the sister relationship between Theoideae and Ternstroemioideae as well as the monophyly of Ternstroemioideae.

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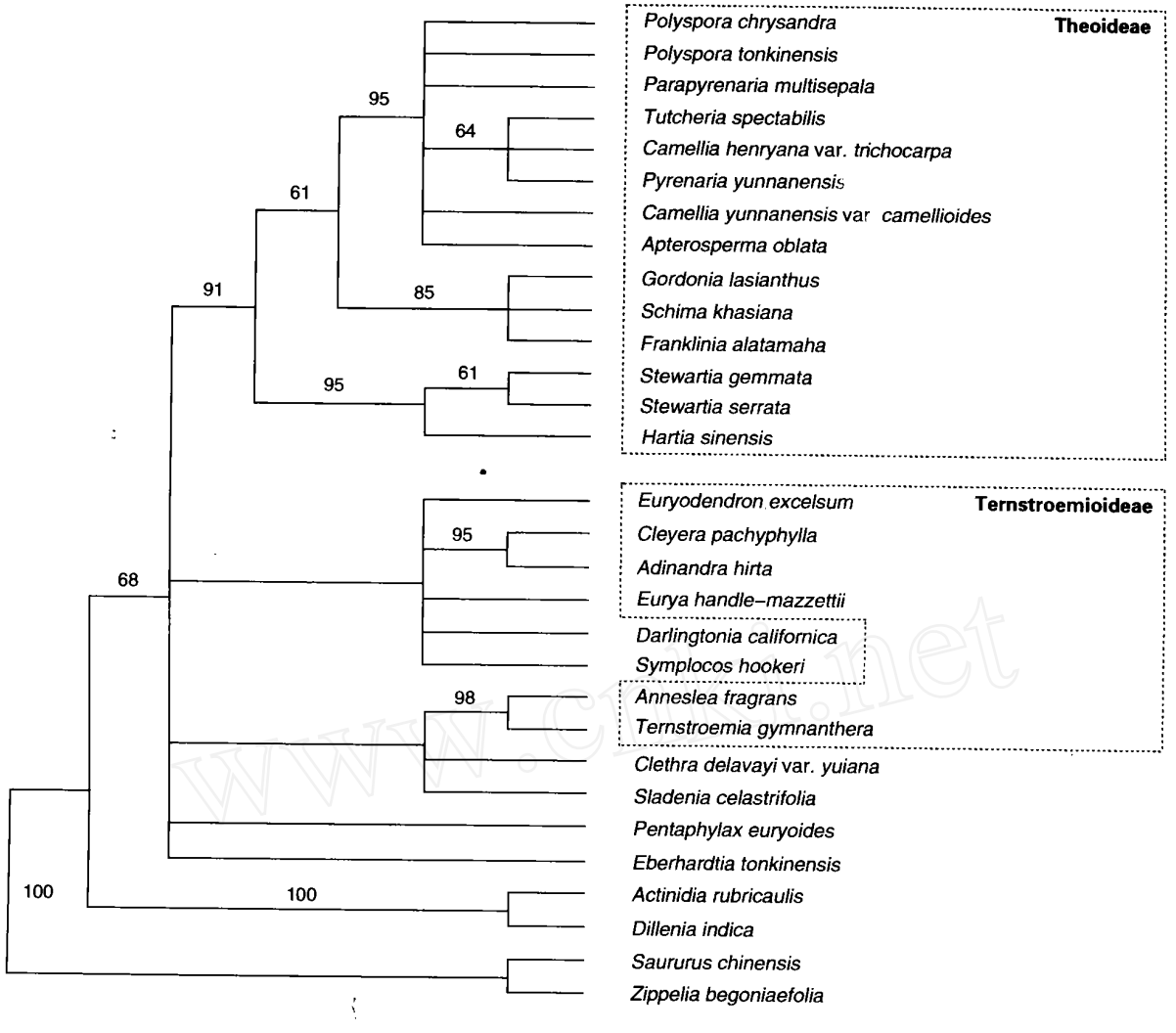

Fig. 3 The best maximum likelihood tree based on the *mat*R gene sequences data (-Ln likelihood = 3836.66389). Numbers above the lines represent the bootstrap values in 1000 replicates

Discussion

The circumscription of Theaceae

Recent phylogenetic analyses based on DNA sequence data (Morton *et al*. 1996, 1997; Savolainen *et al*. 2000; Soltis *et al*. 2000; Prince and Parks, 2001; Anderberg *et al*. 2002) suggest that subfamilies Theoideae and Ternstroemioideae each are monophyletic, but the Theaceae sensu lato is paraphyletic. This has led to the recognition of two individual families, Theaceae sensu stricto (s.s.) and Ternstroemiaceae. In the *mat*R phylogenies, Theoideae form a well supported clade, while the relationships of Ternstroemioideae are either unresolved (Fig. 1, 3) or is resolved as paraphyletic with weak bootstrap support (Fig. 2). Subfamily Ternstroemioideae has been shown to be monophyletic in chloroplast DNA sequence analyses (Prince and Parks, 2001). However, the support for the monophyly of this subfamily was weak. Therefore, further study is warranted to test this hypothesis. Nevertheless, our results are consistent with previous analyses in recognizing the Theaceae s.s. Therefore, Theaceae s.s. will be used in the following discussion.

The tribal and subtribal classification within Theaceae

The tribal and generic relationships within the family Theaceae have been in debate. Several hypotheses of relationships within Theaceae have been proposed (Table 2). Most authors recognize at least two tribes or sub-

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tribes, but the specific composition varies considerably from one system to another. (e.g. Airy-Shaw, 1936; Keng, 1962; Ye, 1990; Chang, 1998; Tsou, 1998; Prine and Parks, 2001).

Table 2　Different taxonomic systems of the family Theaceae s.s.

Airy-Shaw (1936)	Sealy (1958)	H. Keng (1962)	Melchior (1964)	C. X. Ye (1990)	H. T. Chang (1998)	C. H. Tsou (1998)	Prince & Parks (2001)
I. Camellieae	Camellieae	I. Stuartieae	I. Theeae	I. Theeae	I. Theeae	I. Camellieae	I. Theeae
Ia. Camelliinae	a. Cordoniinae	*Stuartia*	*Piquetia*	*Camellia*	*Camellia*	*Camellia* s.l.	*Camellia* s.l.
Piquetia	*Gordonia*	*Hartia*	*Camellia*	II. Pyrenarieae	Tutcheria	*Polyspora*	Pyrenaria s.l.
Stereocarpus	*Laplacea*	II. Cordonieae	Pyrenaria	Tutcheria	II. Cordonieae	(incl. ?*Laplacea*)	*Polyspora*
Camellia	b. Schiminae	IIa. Cordoniinae	*Polysporia*	Pyrenaria	*Gordonia*	Pyrenaria s.l.	*Laplacea*
Tutcheria	*Stuartia* s.l.	*Gordonia*	*Laplacea*	Parapyrenaria	*Schima*	(incl. Tutcheria or	*Apterosperma*
Ib. Laplaceinae	*Schima*	*Laplacea*	II. Cordonieae	III. Cordonieae	*Apterosperma*	? Parapyrenaria)	II. Cordonieae
Laplacea	*Franklinia*	IIb. Schiminae	*Gordonia*	*Polyspora*	III. Stewartieae	Sinopyrenaria	*Gordonia* s.s.
Pyrenaria	c. Camelliinae	*Schima*	*Franklinia*	*Gordonia*	*Hartia*	II. Cordonieae	*Franklinia*
Polysporia	Pyrenaria	*Franklinia*	*Schima*	*Laplacea*	*Stewartia*	IIa. Stewartieae	*Schima*
II. Cordonieae	*Yunnanea*	III. Camellieae	*Stewartia*	IV. Schimeae	IV. Pyrenarieae	*Hartia*	III. Stewartieae
IIa. Stewartiinae	Tutcheria	IIIa. Camelliinae		*Schima*	Pyrenaria	*Stewartia*	*Stewartia* s.l.
Stewartia s.l.	*Camellia*	*Camellia*		*Apterosperma*	Parapyrenaria	IIb. Cordonieae	
IIb. Cordoniinae		*Stereocarpa*		*Franklinia*		*Gordonia* s.s.	
Franklinia		*Yunnanea*		V. Stewartieae		*Schima*	
Gordonia s.s.		IIIb. Pyrenariinae		*Stewartia*		*Apterosperma*	
Schima		Tutcheria		*Hartia*		*Franklinia*	
		Pyrenaria					

In the *mat*R phylogenies (Figs. 1 - 3), Three major clades are recognized, which is consistent with Prince and Parks (2001). The Stewartieae clade includes *Hartia* and *Stewartia*, the Cordonieae clade contains *Gordonia*, *Schima* and *Franklinia*, and the Theeae clade is composed of *Camellia*, *Polyspora*, *Pyrenaria* s.l. and *Apterosperma*. In the chloroplast gene phylogenies (Prince and Parks, 2001), the three clades, Theeae, Cordonieae and Stewartieae, form a trichotomy. In our *mat*R-based phylogenetic trees (Figs. 1 - 3), the Cordonieae clade is more closely related to Theeae than to Stewartieae, supporting Keng's (1962) hypothesis that Stewartieae is least specialized group in Theaceae. In contrary, many classification systems place Theeae in the basal position (Airy-Shaw, 1936; Melchior, 1964; Ye, 1990; Chang, 1998; Tsou, 1998). However, the support for the sister relationship between Theeae and Cordonieae is weak (bs = 64 %), indicating that more data are needed to further test this relationship.

Apterosperma is a monotypic genus established by H. T. Chang in 1976 and has been placed close to *Schima* (Ye, 1990; Chang, 1998; Tsou, 1998). Prince and Parks (2001) revealed that *Apterosperma* was not grouped with *Schima* and was distributed in Theeae, which is supported by the present *mat*R analysis as well as our combined analyses of molecular data from the nuclear, plastid and mitochondrial genomes (Yang *et al*., 2004).

The utility of mat R sequence data in the phylogenetic analysis of Theaceae

In the *mat*R-based phylogenetic trees (Figs. 1 - 3), there were few well-supported clades at the generic level. *Camellia* and *Polyspora* did not form monophyly respectively, so did the *Pyrenaria* s.l. consisting of these kindred genera: *Pyrenaria*, *Tutcheria* and *Parapyrenaria*. All these further verify the hypothesis that *mat*R is useful to reconstruct higher-level phylogeny, such as the relationships of orders, families, or distant genera (Qiu *et al*. 1999; Meng *et al*. 2002).

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