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Leaf epidermal features of *Quercus* subgenus *Cyclobalanopsis* (Fagaceae) and their systematic significance

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Leaf epidermal features are important taxonomic features in *Quercus*. We studied leaf epidermal features of 91 species and one forma of *Quercus* subgenus *Cyclobalanopsis* using light and scanning electron microscopy. Trichome terminology in oaks was assessed and clarified, aiming to score the epidermal features accurately for genus-wide comparison. Nine trichome types, anomocytic and cyclocytic stomatal apparatus, smooth layer and platelet epicuticular wax flakes, and two trichome base types were found in subgenus *Cyclobalanopsis*. The epidermal features revealed three main groups in subgenus *Cyclobalanopsis*. The epidermal features of *Quercus s.l.* were uniform, supporting recognition of *Cyclobalanopsis* as a subgenus of *Quercus* rather than as a separate genus. Most leaf epidermal features show a mosaic pattern, although their numerous variations offered valuable resources for species identification. The leaf epidermal features that can be used for identification of *Quercus* leaves are also discussed and summarized. © 2014 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2014, **176**, 224–260.

ADDITIONAL KEYWORDS: anatomy – evergreen oak – light microscope – SEM – trichome.

INTRODUCTION

Leaf epidermal features are diverse and abundant in flowering plants, making them ideal subjects for investigations of plant morphology and anatomy and also for providing information on taxonomy, ecology, physiology, and development (Payne, 1978; Leaf Architecture Working Group, 1999). *Quercus* L. (oaks) is the largest genus in Fagaceae. Subgenera *Quercus* and *Cyclobalanopsis* (Oerst.) Schneid. are distinguished from one another based on the appearance in the latter of imbricated scales or lamellae on the cupule (Camus, 1934–1954). Subgenus *Cyclobalanopsis*, with approximately 90 (Deng, 2007) to 122 species (Govaerts & Frodin, 1998), is one of the dominant woody genera in broad-leaf evergreen forests of tropical and subtropical East and South-East Asia.

Leaf epidermal features have been widely used for identification of oak species and higher-level oak taxa (Soepadmo, 1972; Manos, 1993; Huang, Chang & Bartholomew, 1999; Nixon, 2002). Camus (1934–1954) comprehensively studied the morphology and taxonomy of Fagaceae. Her work offered a great contribution to the anatomy and underpins much of modern Fagaceae taxonomy. In her monograph, a large number of leaf anatomical features were illustrated in line drawings, including the basic trichome types and leaf venation patterns. However, the fine-

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scale epidermal features could not be as readily studied or represented in Camus's time, until the scanning electron microscope (SEM) came into broad use in the 1960s and 1970s. Hardin (1975, 1976, 1979) used SEM to document leaf trichome variation in the North American oak species. Jones (1986) studied the leaf epidermal features of all genera of Fagaceae. These works established a terminology of leaf epidermal features of Fagaceae. Subsequently, the leaf epidermal features of a large number of oaks from Europe and Asia have been reported, especially from the Mediterranean region (Llamas *et al*., 1995; Zhou, Wilkinson & Wu, 1995; Bussotti & Grossoni, 1997; Uzunova, Palamarev & Ehrendorfer, 1997; Luo & Zhou, 2001; Karioti *et al*., 2011; Panahi *et al*., 2012), Tschan & Denk, 2012). All these studies form a solid foundation for comparative analysis of the leaf epidermal features of this large genus.

However, leaf epidermal studies conducted on subgenus *Cyclobalanopsis* have been limited in scope and sampling. Jones (1986) surveyed epidermal features across Fagaceae, documenting leaf epidermal features of 12 species of subgenus *Cyclobalanopsis*. More comprehensive studies were conducted by Luo & Zhou (2001), who identified eight trichome types (not including papillae) in a comparative study of leaf epidermal features in 48 species of subgenus *Cyclobalanopsis*. Deng, Coombes & Li (2011) compared leaf epidermal features of five closely-related species of subgenus *Cyclobalanopsis* subsection *Chrysotrichae* Menitsky and clarified the taxonomy of those species. These studies demonstrated that leaf epidermal features are taxonomically and phylogenetically informative in subgenus *Cyclobalanopsis*, but all were either geographically restricted or limited in sampling. Leaf epidermal features in subgenus *Cyclobalanopsis* have thus not been comprehensively assessed.

Leaf cuticle features may be phylogenetically conservative or, conversely, exhibit a low phylogenetic signal as a result of convergence, and it is difficult to undertake comparative studies of leaf morphology without a good understanding of homology and a common terminology. Leaf epidermal features of *Quercus s.l.* were well recorded in previous studies, although the terminologies of the leaf epidermal features in different studies were not entirely consistent, especially for trichome types (Table 1). Such inconsistencies in trichome terminology have made comparative studies of trichomes on the leaf epidermis in *Quercus s.l.* difficult.

The present study aimed to: (1) refine leaf trichome terminology in oaks; (2) document leaf epidermal features of subgenus *Cyclobalanopsis* using light microscopy (LM) and SEM; (3) assess the phylogenetic and taxonomic significance of leaf epidermal features; and (4) survey leaf epidermal features of *Quercus s.l.*, with a focus on *Cyclobalanopsis*, to identify phylogenetic patterns.

MATERIAL AND METHODS

Plant materials for the present study were collected from 101 herbarium specimens at BM, CSH, K, KUN, P, and SWFC, representing 91 species and one forma of subgenus *Cyclobalanopsis* (Table 2). The authors of plant names are provided in Table 2. All materials were examined using LM and SEM. All slide mounts are deposited in the herbarium of Shanghai Chenshan Plant Science Research Center, Chinese Academy of Sciences, China (CSH).

Leaf epidermal materials for LM were prepared from mature leaves. Leaf segments (1.0 × 1.0 cm) were boiled in water for 2 min to remove epicuticular wax and then macerated overnight (> 12 h) in 1 : 1 (by volume) hydrogen dioxide (= hydrogen peroxide) solution and glacial acetic acid at 60 °C. The cleared leaf cuticles were stained with 1% safranin-alcohol (m/v, in 50% ethanol) for 5 h before mounting in glycerin gel. Prepared cuticles were observed using an Olympus microscope (Model BX53).

The material (1.0 × 1.0 cm leaf segments) for SEM observation was directly mounted on stubs without any treatment, and after sputter-coating with gold, the specimens were examined and photographed under an SEM (Model S-3400N; Hitachi).

The size of the trichome and trichome base and the length and width of the stomata were measured under × 400 magnification from five random field images in IMAGEJ (Schneider, Rasband & Eliceiri, 2012: http://rsbweb.nih.gov/ij/). The descriptions and terminologies of trichomes and leaf epidermal cells mainly follow Dilcher (1974), Hardin (1976, 1979), Jones (1986) and Tschan & Denk (2012). Stomatal apparatus were classified *sensu* Dilcher (1974). The classification and description of epicuticular wax structures followed that reported by Barthlott *et al*. (1998).

The selected leaf epidermal morphological features of 13 species of subgenus *Cyclobalanopsis* were obtained from the present study. The characters of three species of *Quercus* section *Cerris* Loudon (*Quercus acrodonta* Seemen, *Quercus utilis* Hu & W.C.Cheng, and *Quercus aquifolioides* Rehder & E.H.Wilson) were from Zhou, Wilkinson & Wu (1995) and Yang, Dong & Zhao (2012). These data were mapped onto the phylogeny using the neighbor joining (NJ) method and were also used to produce a morphological cladogram. The states of selected morphological characters were mainly coded as absent (0) or present (1). Transitions were reconstructed on a previous internal transcribed spacer (ITS) molecular phylogenetic study ofDeng, Zhou & Li (2013b) using parsimony in MESQUITE, version 2.75 (Maddison & Maddison, 2011)

Table 1. Trichome classification in *Quercus* subgenus *Cyclobalanopsis*: comparison of our proposed terminology with that of previous studies

Author	Trichome types described in previous studies	Trichome types proposed in the present study	Figures (present study)
Camus (1938–1954)	Poils unicellulaires isoles	Solitary	162
	Poils fascicules a articles concrescents	Stipitate fasciculate (SF)	133–138
	Poils fascicules en bouquets, ou buissons, a articles libres	Fasciculate (F)	125, 127, 128, 161, 162
	Poil étoilé	Simplified stellate (SSt) and stellate (St)	SSt: 117–120, 122–124, 126, 128, 129–132, 158–160, 182, 183; St: 139–145, 184–186
	Poils ecailleux ou en ecusson	Stellate (St)	139–145, 184–186
	Poils unicellulaires apprimes, en navette	Appressed laterally attached	85, 106–116, 121, 128, 151–158
	Poil sécréteur	Mixture of uniseriate (U), capitate and branched uniseriate (BU)	U: 37–40, 43, 47, 49, 51, 56, 61, 63, 67, 71, 74, 75, 78, 86, 88–102, 112, 114, 170, 172–180, 182, 187–193, 195; BU: 60, 103–105, 163–168
Hardin (1976)	Simple-uniseriate	Uniseriate	37–40, 43, 47, 49, 51, 56, 61, 63, 67, 71, 74, 75, 78, 86, 88–102, 112, 114, 170, 172–180, 182, 187–193, 195
	Simple-branched	Branched uniseriate	60, 103–105, 163–168
	Bulbous	Mixture of capitate (Ca) and uniseriate (U)	U: 195
	Rosulate	Rosulate	146, 147, 191, 192, 195
	Solitary	Solitary	162
	Appressed-lateral	Appressed laterally attached	85, 106–116, 121, 128, 151–158
	Fasiciculate	Mixture of stipitate fasciculate (SF) and fasciculate (F)?	SF: 133–138; F: 125, 127, 128, 161, 162
	Multiradiate	Stellate (St)	139–145, 184–186
	Stellate	Simplified stellate (SSt)	117–120, 122–124, 126, 128, 129–132, 158–160, 182, 183
	Fused-stellate	Stellate (St)	139–145, 184–186
Jones (1986)	Type 1 (solitary unicellular)	Solitary	162
	Type 3 (papillae)	Thickenings on the epidermal cells, not trichomes	Not trichomes 70–85, 98, 99, 103, 110–111
	Type 4 (appressed laterally attached unicellular)	Appressed laterally attached	85, 106–116, 121, 128, 151–158
	Type 5 (fasciculate)	Fasciculate	125, 127, 128, 161, 162
	Type 6 (stellate)	Simplified stellate	117–120, 122–124, 126, 128, 129–132, 158–160, 182, 183
	Type 7 (fused stellate)	Stellate	139–145, 184–186
	Type 8 (stipitate fasciculate)	Stipitate fasciculate	133–138
	Type 10 (multiradiate)	Stellate	139–145, 184–186
	Type 14 (Rosulate)	Rosulate	146, 147, 191, 192, 195
	Type 15 (simple uniseriate)	Uniseriate	37–40, 43, 47, 49, 51, 56, 61, 63, 67, 71, 74, 75, 78, 86, 88–102, 112, 114, 170, 172–180, 182, 187–193, 195
	Type 16 (capitate or irregularly multiseriate)	Capitate	–
	Type 18 (branched uniseriate)	Branched uniseriate	60, 103–105, 163–168

Table 1. *Continued*

Author	Trichome types described in previous studies	Trichome types proposed in the present study	Figures (present study)
Zhou *et al*. (1995)	Unbranched glandular	Uniseriate	37–40, 43, 47, 49, 51, 56, 61, 63, 67, 71, 74, 75, 78, 86, 88–102, 112, 114, 170, 172–180, 182, 187–193, 195
	Branched glandular	Branched uniseriate	60, 103–105, 163–168
	Fasiciculate	Stipitate fasciculate	133–138
	Stellate	Simplified stellate	117–120, 122–124, 126, 128, 129–132, 158–160, 182, 183
	Stalked stellate	Stellate	139–145, 184–186
Llamas *et al*. (1995)	Simple uniseriate	Uniseriate	37–40, 43, 47, 49, 51, 56, 61, 63, 67, 71, 74, 75, 78, 86, 88–102, 112, 114, 170, 172–180, 182, 187–193, 195
	Bulbous	Capitate	–
	Solitary	Solitary	162
	Fasciculate	Mixture of fasciculate (F) and Stipitate fasciculate (SF)	SF: 133–138; F: 125, 127, 128, 161, 162
	Multiradiate	Stellate	139–145, 184–186
	Stellate	Simplified stellate	117–120, 122–124, 126, 128, 129–132, 158–160, 182, 183
	Fused stellate	Stellate	139–145, 184–186
Bussotti & Grossoni (1997)	Fasiciculate-stipitate	Stipitate fasiciculate	133–138
	Stellate	Mixture of simplifed stellate (SSt) and stellate (St)	SSt: 117–120, 122–124, 126, 128, 129–132, 158–160, 182, 183; St: 139–145, 184–186
	Multiradiate	Stellate	139–145, 184–186
	Bulbous	Capitate	–
	Simple uniseriate	Uniseriate	37–40, 43, 47, 49, 51, 56, 61, 63, 67, 71, 74, 75, 78, 86, 88–102, 112, 114, 170, 172–180, 182, 187–193, 195
Uzunova *et al*. (1997)	Secretory capitate	Capitate	–
	Secretory uniseriate	Uniseriate	37–40, 43, 47, 49, 51, 56, 61, 63, 67, 71, 74, 75, 78, 86, 88–102, 112, 114, 170, 172–180, 182, 187–193, 195
	Stellate	Simplified stellate	117–120, 122–124, 126, 128, 129–132, 158–160, 182, 183
	Stellate on pedestal 'ilex' type	Stellate	139–145, 184–186
	Fasciculate	Fasciculate	125, 127, 128, 161, 162
	Stipitate fasciculate	Stipitate fasciculate	133–138
	Simple, single	Solitary	162
Luo & Zhou (2001)	Solitary trichome	Mixture of solitary (S), appressed laterally attached (ALA) and uniseriate (dark stained multicelluar uniseriate) (U)	S: 162; ALA: 85, 106–116, 121, 128, 151–158; U: 37–40, 43, 47, 49, 51, 56, 61, 63, 67, 71, 74, 75, 78, 86, 88–102, 112, 114, 170, 172–180, 182, 187–193, 195
	Papillae	Thickenings on the epidermal cells, not trichomes	Not trichomes 70–85, 98, 99, 103, 110–111
	Stellate trichome	Simplified stellate	117–120, 122–124, 126, 128, 129–132, 158–160, 182, 183

Table 1. *Continued*

Author	Trichome types described in previous studies	Trichome types proposed in the present study	Figures (present study)
	Fused stellate trichome	Stellate	139–145, 184–186
	Multiradiate trichome	Stellate	139–145, 184–186
	Jellyfish-like trichome	Rosulate	146, 147, 191, 192, 195
	Simple uniseriate trichome	Uniseriate	37–40, 43, 47, 49, 51, 56, 61, 63, 67, 71, 74, 75, 78, 86, 88–102, 112, 114, 170, 172–180, 182, 187–193, 195
Panahi *et al*. (2012)	Simple-uniseriate	Uniseriate	37–40, 43, 47, 49, 51, 56, 61, 63, 67, 71, 74, 75, 78, 86, 88–102, 112, 114, 170, 172–180, 182, 187–193, 195
	Bulbous	Capitate	–
	Solitary	Solitary	162
	Fasciculate (sessile)	Fasciculate	125, 127, 128, 161, 162
	Fasciculate (stipitate, pedestaled)	Stipitate fasciculate	133–138
	Stellate	Mixture of simplified stellate (SSt) and stellate (St) ?	SSt: 117–120, 122–124, 126, 128, 129–132, 158–160, 182, 183; St: 139–145, 184–186
Tschan & Denk (2012)	Acicular (‘whip’)	Mixture of solitary (S) and appressed laterally attched (ALA)?	S: 162; ALA: 85, 106–116, 121, 128, 151–158
	Bifurcate (‘fork)	Simplified stellate	117–120, 122–124, 126, 128, 129–132, 158–160, 182, 183
	Fasciculate	Mixture of fasciculate (F) and stipitate fasciculate (SF)	F: 125, 127, 128, 161, 162; SF: 133–138
	Stellate	Mixture of simplified stellate (SSt) and stellate (St)	SSt: 117–120, 122–124, 126, 128, 129–132, 158–160, 182, 183; St: 139–145, 184–186
	Uniseriate	Uniseriate	37–40, 43, 47, 49, 51, 56, 61, 63, 67, 71, 74, 75, 78, 86, 88–102, 112, 114, 170, 172–180, 182, 187–193, 195
	Capitate	Capitate	–

The images of trichome types detected in the present study are listed.

(http://mesquiteproject.org/mesquite/mesquite.html). All characters were treated as unordered, unpolarized, and unweighted. Cladistic analysis on selected coded leaf epidermal characters was performed in PAUP 4.0b10 (Swofford, 2002) using the NJ method. Each character was treated unordered and equal. According to the phylogenetic study of Fagaceae by Oh & Manos (2008), the clade *Castanea* Mill. + *Castanopsis* (D.Don) Spach is the sister group to *Quercus s.l.* We used *Castanopsis indica* A.DC., of which the leaf epidermal features were reported by Liu, Deng & Zhou (2009) (the status of selected leaf epidermal features are listed in Table 3 and Fig. 196B), as an outgroup to root the tree. The stability of the tree topology was tested by bootstrap resampling (Felsenstein, 1985) of 1000 replicates using tree bisection–reconnection branch-swapping on 100 random taxon-addition replicates per bootstrap replicate.

RESULTS

Most leaf epidermal features showed considerable interspecific variation in subgenus *Cyclobalanopsis*, although some characters were phylogenetically strongly conserved or exhibited considerable homoplasy. The degree of interspecific variation suggests considerable potential for future study of adaptation. The detailed leaf epidermal features for each specimen and the trichome dimensions are summarized in Table 3 (see also Supporting information, Table S1).

Table 2. List of species, vouchers and collection localities used for the leaf epidermal study

	Scientific name	Collection locality	Collection	Herbarium for voucher
1	*Quercus albicaulis* Chun & Ko	Shuan-xi-mu Village, Hainan Province, China, 29 October 1933	*Wang, C. 34910*	SWFC
2	*Quercus annulata* Sm.	Khasia, Regio trop, altitude 2–4000 feet, Assam, India	*Hooker, J.D. & Thomson, T. s.n.*	K
3	*Quercus arbutifolia* Hickel & A.Camus	You-po-ji, Mei-Hua-Shan National Nature Reserve, Shang-hang County, Fujian Province, China, on top of the mountain, altitude 1687 m, E 116°49.841′; N 25°20.498′	*Deng, M. et al. 4047*	CSH
4	*Quercus argentata* Korth	Singapore, Bukit Timah Reserve, 4 December 1939	*Ngadiman 319/36398*	BM
5	*Quercus argyrotricha* A.Camus	Tuipo, Picheh, Guizhou Province, China	*Tsiang, Y. 8990*	KUN
6	*Quercus asymmetrica* Hickel & A.Camus	Tonkin. Kne-Va (Hai-Ninh), Vietnam, 27 September 1917	*Casabianca 5*	P
7	*Quercus asymmetrica* Hickel & A.Camus	From Forest Bureau to NanChai Riever, Ba-Wang-Lin National Nature Reserve, Hainan, China, altitude 740 m, E 109°09.358′; N 19°06.581′ (type locality of *Quercus patelliformis*)	*Deng, M. et al. 4249*	CSH
8	*Quercus augustinii* Skan	Shui-wei-chen, Da-Wei-shan National Nature Reserve, Pinbian, Yunnan, China, altitude 1980 m, N 22°59′0.8254″; E 103°41′15.4068″	*Deng, M. 4768*	CSH
9	*Quercus auricoma* A. Camus	Hong-Hua-Tang, Er-Huang-Zhang Nature Reserve, Guangdong, China, altitude 65 m, E 111°31.481′; N 21°55.139′	*Deng, M. et al. 3830*	CSH
10	*Quercus austrocochinchinensis* Hickel & A.Camus	tropical forest, Guangpin Village, Jinhong, Yunnan, China, altitude 800 m, E 100°51′21″; N 22°20′02″	*Deng, M. & Li, Q.J. 4518*	CSH
11	*Quercus austroglauca* (Y.T.Chang) Y.T.Chang	Tou-Pi-Shu, Fadou Village, Xi-chou County, Yunnan Province, China, altitude 1780 m, E 104°40′20.1036″; N 23°26′14.8859″	*Deng, M. & Liu, Y.C. 396-2*	CSH
12	*Quercus bella* Chun & Tsiang	Liu-Xiang River to Wu-Zhi Mount, Guangxi Province, China, the evergreen forest by the roadside, altitude 1200 m, E 110°04.765′; N 23°53.584′	*Deng, M. et al. 4196*	CSH
13	*Quercus blakei* Skan	Wang-Jia Village to Ying-Ge-Lin Nature Reserve, in the evergreen forest, Hainan Province, China, altitude 1115 m; E 109°33.047′; N 19°03.792′	*Deng, M. et al. 3218*	CSH
14	*Quercus braianensis* A.Camus	Grand sommet près du Dantia, E de Dantia, Annam, Vietnam, 13 January 1931	*Poliane, E. 18767*	K
15	*Quercus brandisiana* Kurz	Haohongson, Hae Taeng-Pai, Thailand, altitude 1100–1400 m, 6 December 1977	*Santisuk, T. 1516*	K
16	*Quercus brevicalyx* A.Camus	Pu Bia, altitude 2300 m, Laos, 13 April 1932 (type)	*Kerr, A.F.G. 21017*	K
17	*Quercus brevicalyx* A.Camus	Back hill of Mu-Long-Jin, Sudian, 24 May 1980, altitude 2500 m, Yinjiang, Yunnan, China (type of the synonymous *Quercus yingjiangensis*)	*Yang, S.R. 9*	SWFC
18	*Quercus championii* Benth.	E II logging camp, Ba-Wang-Lin National Nature Reserve, Changjiang, Hainan, China, altitude 1104 m, E 109°11.872′; N 19°05.321′	*Deng, M. et al. 3048*	CSH

Table 2. *Continued*

	Scientific name	Collection locality	Collection	Herbarium for voucher
19	*Quercus chapensis* Hickel. & A.Camus	Pin-Zhai, Faduo Village, Xi-Chou, Yunnan, China, altitude 1750 m, E 104°40′20.1036″; N 23°26′14.8859″	*Deng, M. & Liu, Y.C. 349-15*	CSH
20	*Quercus chrysotricha* A.Camus	Dulit Ridge, shady moss forest, Sarawak,altitude 1300 m, 17 September 1932	*Richards, R.W. 1885*	K
21	*Quercus chrysotricha* A.Camus	Slope of Apo Duat, Kelabit Highland, Baram District, 4th Div., Sarawak	*Chai, P. 35492*	K
22	*Quercus chungii* F.P.Metcalf	Hei-Shi-Ding Nature Reserve, the main entrance to the Nature Reserve, by the river, Feng-kai County, Guangdong Province, China, altitude 115 m, E 111°54′0.14′; N 23°28′33.32′	*Deng, M. et al. 4402*	CSH
23	*Quercus daimingshanensis* (S.Lee) C.C.Huang	Yu-Xian-Tou, Da-Ming Mount., Wuming, Guangxi, China, altitude 1200 m, E 108°26.123′; N 23°30.035′	*Deng, M. et al. 4121*	CSH
24	*Quercus delavayi* Franch.	Gou-Dong Village, Songmin, Kunming, Yunnan, China, altitude 2128 m, E 102°45′19.368″; N 25°18′4.176″	*Deng, M. et al. 3562*	CSH
25	*Quercus disciformis* Chun	Loudong Village, Shangfan District. Da-Miao-Shan, Guangxi, China, 17 July 1958	*Chen, S.Q. 15725*	SWFC
26	*Quercus edithae* Skan	Wdawu pro, altitude 530 m, Mizihkyine, Burma	*Maung Mya5359*	K
27	*Quercus edithae* Skan	Evergreen forest by Bai-Shui waterfall, Diao-lou-shan National Nature Reserve, Lin-shui County, Hainan Province, China, altitude 627 m, N 18°42.057′; E 109°50.765′	*Deng, M. et al. 4322*	CSH
28	*Quercus elmeri* Merr.	Farm Road, Fraser's Hill, Singapore, altitude 3800 feet.	*Purseglove, J.W. 4263*	K
29	*Quercus gaharuensis* Soepadmo	Cunong Mulu National Park, 4th Div. Sarawak, 28 September 1976	*Martin, P.J. s.38017*	K
30	*Quercus gambleana* A.Camus	Cha-Pai logging camp, Xia-Jin-Chang Village, Ma-li-po County, Yunnan Province, China, altitude 2200 m, E 104°42′10.1844″; N 23°7′31.6632″	*Deng, M. & Liu, Y.C. 472*	CSH
31	*Quercus gemelliflora* Blume	Mempening, Fraser's Hill, Pahang, Malaya, 11 November 1937	*Medan 45417*	K
32	*Quercus gemelliflora* Blume	Kemansol, T. Reo. Pahang, Malaya, 8 February 1936	*Kochummen, K.M. 40670*	K
33	*Quercus gilva* Blume	Royal Botanic Gardens, Kew, living collections (introduced from Japan)	*Deng, M. et al. 3660*	CSH
34	*Quercus glabricupula* Barnett	Siam, Doi Intaccou, altitude 1600 m, 1 May 1921	*Kerr, A.F.G. 5295*	K
35	*Quercus glauca* Thunb.	Nagasaki, Japan	*Maximowicz. Iter secundum sn.*	K
36	*Quercus glauca* f. *gracilis* Rehder & E.H.Wilson	W. Hupei, China, September 1907	*Wilson, E.H. 687*	K
37	*Quercus gomeziana* A.Camus	Chittagong Hill tracts, 40 miles from Chittagong, (now in Bangladesh) May 1886	*King 3405*	K
38	*Quercus gomeziana* A.Camus	Unknown	*Brandis, D. 530*	K
39	*Quercus helferiana* A.DC.	on the way to Xu-jia-ba ecolotgical station, Jingdong County, Yunnan Province, China, by the roadside, in evergreen forest, altitude 1430 m, E 100°31.950′; N 22°59.785′	*Deng M. et al. 2044*	CSH

Table 2. *Continued*

	Scientific name	Collection locality	Collection	Herbarium for voucher
40	*Quercus hondae* Makino	Tsuruta-Dam, Tsuruta-Mura, Satsuma-gun prov. Satsuma, Japan.	*Miyoshi Fuduse 10225*	K
41	*Quercus hypargyrea* (Seemen ex Diels) C.C.Huang & Y.T.Chang	Bai-Shan-Zhu National Nature Reserve, Li-Shui County, Zhejing Province, China, altitude 1376 m, N 27°45.086′, E 119°11.554′	*Deng, M. et al. 3885*	CSH
42	*Quercus jenseniana* Hand.-Mazz.	You-Po-Ji, Mei-Hua-Shan National Nature Reserve, in the ravine, evergreen forest, Shanghang County, Fujian Province, China, altitude 1300 m, E 116°50.367′; N 25°20.590′	*Deng, M. et al. 4032*	CSH
43	*Quercus kerangasensis* Soepadmo	Borneo, May 1898	*Haviland, G.D. 1172*	K
44	*Quercus kerrii* Craib.	Nan-cha River, Ba-Wang-Lin National Nature Reserve, Chang-jiang County, Hainan Province, China, altitude 994 m, 17 November 2012, E 100°53.130′; N 22°15.832′.	*Deng, M et al. 2014*	CSH
45	*Quercus kinabaluensis* Soepadmo	Sample plot II, west of Mesilsu Cave, Sandakan, Sabah, Borneo, altitude 8000 feet, 21 February 1965.	*Meijer, W. 48115(NT938)*	K
46	*Quercus kiukiangensis* (Y.T.Chang) Y.T.Chang	Shui-wei-chen, Da-Wei-shan National Nature Reserve, Pinbian County, Yunnan Province, China, altitude 1980 m, N 22°59′0.8254″; E 103°41′15.4068″	*Deng, M. & Liu, Y.C. 300*	CSH
47	*Quercus kouangsiensis* A.Camus	Xing-An Village, Diao-Luo-Shan Nature reserve, Lin-shui County, Hainan Province, China, altitude 914 m, 25 June 2012	*Deng, M. et al. 3339*	CSH
48	*Quercus lamellosa* Sm.	Manipur, eastern frontier of India, altitude 6900 feet, 2 December 1883	*Watt, G. 6219*	K
49	*Quercus lamellosa* Sm.	Chevithorne Barton living collection	*Deng, M. et al. 3736*	CSH
50	*Quercus langbianensis* Hickel & A.Camus	Shui-wei-chen, Da-Wei-shan National Nature Reserve, Pinbian County, Yunnan Province, China, altitude 1980 m, E 103°41′15.4068″; N 22°59′0.82536″	*Deng, M. & Liu, Y.C. 301*	CSH
51	*Quercus lineata* Blume	between Smoking house and forest dept. road side, Cameron Highlands, Pahang, Malaysia, altitude 4700 feet	*Bio RAJAB (MOHD, Kasim) 607*	K
52	*Quercus lineata* Blume	Cameron Highlands; Sungei Pauh valley, Malaysia, altitude 5000 feet, E 101° 23′; N 4°29′	*Chew, W.L. 804*	K
53	*Quercus litseoides* Dunn	Lantao, altitude 2000 feet, Hongkong, 16 Mar. 1909.	*Anonymous 6597*	BM
54	*Quercus lobbii* Ettingsh.	Nepal, 4000, 12 November 1871	*Clarke, C.B. 15451*	K
55	*Quercus lobbii* Ettingsh.	Sezarum Khasia Hill, East Bengal, 5000 feet.	*Mause, G. 445-8*	K
56	*Quercus longistyla* Barnett	Kao Krading, Loi, Siam, Thailand, altitude 1200 m (type)	*Kerr, A.F.G. 8708*	K
57	*Quercus lowii* King	Penibukan, jungle ridge, altitude 4500 feet, 2 October 1933, upper Kinabalu, Borneo	*Clemens, J. & M.S. 40699*	K
58	*Quercus macrocalyx* Hickel & A.Camus	East II logging camp, Ba-wang-lin National Nature Reserve, Chang-Jiang, Hainan, China, altitude 1104, E 109°11.872′; N 19°05.321′	*Deng, M. et al. 3049*	CSH

Table 2. *Continued*

	Scientific name	Collection locality	Collection	Herbarium for voucher
59	*Quercus merrillii* Seemen	Puerto Princesa (Mt. Pulgar). Province of Palawan, Philippines, May 1911	*Elmer, A.D.E. 13219*	K
60	*Quercus mespilifolia* Wall. ex A.DC.	Ta Kanun, Kanburi, Siam, Thailand, altitude 400 m, 21 January 1926	*Alan 10284*	K
61	*Quercus mespilifolia* Wall. ex A.DC.	A. Trome mont. 1826; B. Joong Dong 1828, Myanmar	*Wallich, N. 2766*	K
62	*Quercus miyagii* Koidz.	Ryukyu Islands, Japan	*Setoguchi, H. 770*	KUN
63	*Quercus morii* Hayata	Counildu, prov. Kangiyuan,Taiwan, altitude 21660–2666 m, 31 January 1918	*Wilson, E.H. 9700*	K
64	*Quercus motuoensis* C.C.Huang	De-Er-Gong, Motou, Tibet, in evergreen forest on the slope, altitude 1700 m, 10 September 1974	*Qinghai-Tibet Exped. 5069*	PE
65	*Quercus myrsinifolia* Blume	Gong-Mu Village, Wu-Yi-Shan National Nature Reserve, FuJian Province, China, altitude 779 m, E 117°40.401′; N 27°43.982′	*Deng, M. et al. 3936*	CSH
66	*Quercus neglecta* (Schott.) Koidz.	Xin-An Village, Diao-Luo-Shan National Nature Reserve, Lin-Shui, Hainan, China, altitude 607 m, E 109°50.825′; N 18°41.520′	*Deng, M. et al. 3364*	CSH
67	*Quercus ninganensis* (W.C.Cheng & Y.C.Hsu) C.C.Huang	from Chen-Jiao- to the top of Nan-Lin, Nan-Lin, Ruyuan, Guangdong, China, altitude 660 m, E 112°55′53.36″; N 24°51′57.49″	*Deng, M. et al. 4908*	CSH
68	*Quercus nivea* King	Mandi Angin expedition, Ulu s. Loh, Terengganu, Malaysia. ridge top primary forest; altitude 2350 m, 13 July 1968	*Cockburn, P.F. 10838*	K
69	*Quercus oidocarpa* Korth.	Frasers Hill-Gap road, Mile 61 1/4; Malaya, altitude 3500 feet, 26 December 1963	*Poore, M.E.D. 1378*	K
70	*Quercus oxyodon* Miq.	Hou-Shao-Liang-Zi Nature Reserve, Ma-li-po, Yunnan, China, altitude 2150 m, E 104°42′10.1844″; N 23°7′31.6632″	*Deng, M. & Liu, Y.C. 371*	CSH
71	*Quercus pachyloma* Seemen	Feng-Huang Mount, Rao-Pin, Guangdong Province, China, altitude 500 m, E 116°56′31.9568″; N 23°52′9.1517″	*Deng, M. et al. 2084*	CSH
72	*Quercus percoriacea* Soepadmo	S. slope at the east of the helipad from 910 to 990 m elevation, Bukit Tudal, Temburong subdistric Amo, Brunei, Malaysia, 6 October 1994	*Kirkup, D.W. 974*	K
73	*Quercus phanera* Chun	Bai-Shui-Tai waterfall, Diao-Luo-Shan National Nature Reserve, Hainan Province, China, altitude 700 m, E 109°52.974′; N 18°43.013′	*Deng, M. et al. 4294*	CSH
74	*Quercus pseudoverticillata* Soepadmo	Mesilau trail, Kinabalu National park, Ranau, Sandakan, Sabah, altitude 6100 feet	*Chow & Leopold 76409*	K
75	*Quercus quangtriensis* Hickel & A.Camus	Sai Wong Mo Shan (Sai Vong Mo Leng) Lomg Ngong Village Dam-ha, Tonkin, Vietnam, 18 July to 9 September 1940	*Wang, W.T. 30470*	K
76	*Quercus ramsbottomii* A.Camus	Forest near Mularjct, Amherst, Burma, altitude 6300 feet, 3 February 1927	*Parkinson, C. E. 5161*	K
77	*Quercus rex* Hemsl.	Nan-Xian River, Cai-Yuang-He Nature Reserve, Pu-Er, Yunnan, China, altitude 1305 m, E 101°03.342′; N22°36.353′	*Deng, M. et al. 47574*	CSH
78	*Quercus rupestris* Hickel & A.Camus	massif de bô inh, près [Nhakang], Thailand (type)	*Poilane, E. 3627*	K
79	*Quercus salicina* Blume	Chevithorne Barton living collection	*Deng, M. 3700*	CSH

Table 2. *Continued*

	Scientific name	Collection locality	Collection	Herbarium for voucher
80	*Quercus salicina* Blume	Lou-ba Village, Che-Ba-Lin Nature Reserve, Shi-xing County, Guangdong Province, China, 12 November 2012, altitude 445 m, N 24°49′19.00″; E 114°14′40.33″	*Deng, M. 4727*	CSH
81	*Quercus schottkyana* Rehder & E.H.Wilson	Wu-liang Mount, Jingdong County, Yunnan Province, China, altitude 1805 m, E 101°09.287′; N 24°13.827′	*Deng, M. et al. 2072-15*	CSH
82	*Quercus semiserrata* Thunb.	Khasia, Mae Keii valley, upper ridge near Ban Bank Olumy (Mee) Village, Mao Moi, Subdistrict, Thailand, altitude 1400 m, 13 December 1990	*Maxwell, J.F. 90–1340*	IBSC
83	*Quercus sessilifolia* Blume	By the stream, Gua-Deng Village, Wu-Yi Shan National Nature Reserve, Wu-yi-shan city, Fu-jian Province, China, altitude 1500 m, E 117°42.133′; N 27°48.556′	*Deng, M. et al. 3956*	CSH
84	*Quercus sichourensis* (Hu) C.C.Huang & Y.T.Chang	Pin-Zhai, Faduo Village, Xi-Chou County, Yunnan Province, China, altitude 1750 m	*Deng, M. & Liu, Y.C. 356*	CSH
85	*Quercus steenisii* Soepadmo	Climbing Gunung Leuser West top, from Penosan via Putjuk Angasan; approximately 25 km SW of Blang Kedjeren, Gunung Leuser Nature Reserve, Atjeh, North Sumatra, altitude 3100–3420 m, 9 April 1975	*Wilde W.J.J.O. de & Wilde-Duyfjes, B.E.E. de 16261*	K
86	*Quercus stenophylloides* Hayata	Chevithorne Barton living collection, originated from Taiwan	*Deng, M.*	CSH
87	*Quercus stewardiana* A.Camus	Mao-Er-Shan, Xin-an County, Guangxi Province, China, altitude 1930 m, E 126.9181395; N 41.8120033	*Deng, M. et al. 3780*	CSH
88	*Quercus* stewardiana A.Camus	Qian-Jia-Zhai Nature Reserve, ZhengYuan, Yunnan, China, altitude 2184 m, E 101°15.832′; N 24°16.397′ (type locality of *Cyclobalanopsis stewardiana* var. *longicaudata*)	*Deng, M. et al. 2065*	CSH
89	*Quercus subsericea* A.Camus	Cape Richado, Port Dickson. sea-shore along the drift line, Malaya, 28 December 1964	*University of Malaya 636*	K
90	*Quercus sumatrana* Soepadmo	KTC Tumbang Sah, km 96, Katingan River, Borneo, altitude 100 m, E 113° 10′; S 1° 15′, 4 February 1983	*Wiriadinata 3541*	K
91	*Quercus tenuicupula* (Y.C.Hsu & H.W.Jen) C.C.Huang	Weng-dang Village, Jin-pin County, Yunnan Province, China, 27 November 1976	*Zhao, W.S. 1*	SWFC
92	*Quercus thomsoniana* A.DC.	Sikkim, India, altitude 1829–2438 m	*Hooker, J.D. s.n.*	K
93	*Quercus thorelii* Hickel & A.Camus	Nanxian River, MongYang, Jinhong, Xi-shan-ban-na National Nature Reserve, Yunnan Province, China, altitude 701 m, E 100°45′46″; N 22°19′00″	*Deng, M. et al. 4646*	CSH
94	*Quercus tiaoloshanica* Chun & W.C.Ko	Xin-An Village, Diao-Luo-Shan National Nature Reserve, Ling-shui County, Hainan Province, China, altitude 916 m, E 109°52.733′; N 18°43.162′	*Deng, M. et al. 3332*	CSH

Table 2. *Continued*

	Scientific name	Collection locality	Collection	Herbarium for voucher
95	*Quercus tomentosinervis* (Y.C.Hsu & H.W.Jen) C.C. Huang	Yongping Village, Jin-pin County, Yunnan Province, China, May, 1975 (type materials)	*Jen, H.W. 74964*	SWFC
96	*Quercus tranninhensis* Hickel & A.Camus	Jam-neua, Laos, 11 October 1920	*Poilane, M. 2048*	K
97	*Quercus treubiana* Seemen	Archipel. Ind. Borneo, Liang Gagang, Malaysia	*Hallier, J.G. 2915*	K
98	*Quercus treubiana* Seemen	In mossy forest, peak of Balikpapan; Berikanbulu, sandstone, altitude 900 m, 11 July 1952, in mossy forest, E. Borneo	*Kostermans, S.A. 7442*	K
99	*Quercus valdinervosa* Soepadmo	G. Mulu National Park, Ulu Sg. Tutoh, 4th Divistion, Sarawak, altitude 6000–6500 feet, 9 February 1976	*Chai, P.S. 35849*	K
100	*Quercus wangsaiensis* Barnett	Nakawn Sritamarat, Songkla, Ban Wangsai, Thailand, approximately 50 m, by stream in evergreen forest	*Kerr, A.F.G. 15862*	K
101	*Quercus xanthotricha* A.Camus	Lao-Tang-Zai, Yunxian Village, Pu-Er County, Yunnan Province, China, in limestone evergreen forest, altitude 1379 m, E 100°39.254′; N 22°57.962′	*He, S.C. 8554*	SWFC

Adaxial leaf surface (Figs 1–36)

The epidermal cells on the adaxial leaf surface were mostly irregular quadrangular to polygonal. Most of the anticlinal walls of the epidermal cells were straight to curved (Figs 1–18). Sinuous to undulate cell walls were found in 16 species (Figs 19–25). Species with sinuous or undulate anticlinal cell walls mostly had ridged wall thickenings.

Foliar trichomes were present on leaves in most species. Adaxial epidermal cells were mostly glabrous on mature leaves, except for *Quercus salicina* with solitary or clustered hairs (Fig. 1). In all species, trichome bases were present on the adaxial epidermis and distinguishable into two types: (1) single-celled trichome base (STB) (usually a dark stained small basal portion of the trichome), present in all species (Figs 1–25); and (2) compound trichome base (CTB), present in 14 species (Figs 26–36). This trichome base is characterized by four to seven dark stained cells arranged in a circle and usually raised to form a pedestal-like structure.

Abaxial leaf surface

Epicuticular waxes (Figs 37–84, 86–94, 97–105, 107, 108, 116, 117, 121)

Two epicuticular wax types were detected. (1) Smooth layer (Figs 37–49, 88) and continuous coverings usually < 1 μm thick without a prominent surface sculpturing is present in 31 specimens of subgenus *Cyclobalanopsis*. (2) Platelet wax decoration (Figs 52–84, 86, 87) is common, and was found in 70 specimens in subgenus *Cyclobalanopsis*, forming flat crystalloids, connected to the surface by their narrow side and arranged in rosettes. All are non-entire platelets (Figs 68, 69, 82, 83) or membranous platelets (Figs 52–67, 70–81). In *Quercus longistyla* (Fig. 50), *Quercus helferiana* (Fig. 51), and *Quercus mespilifolia* (Fig. 89), the wax type was predominantly smoothm but with a few platelet flakes, which were small and thin, appearing intermediate in morphology between the smooth layer and typical platelet layer. Platelet epicuticular wax flakes are easily rubbed away on herbarium specimens, especially on the convex papillae thickenings.

Epidermal cells (Figs 151–195)

The abaxial epidermal cells show great variation in shape, anticlinal wall patterns, and thickening. The epidermal cells are irregular polygons, and most species have straight or curved anticlinal cell walls. The thickness of the anticlinal wall is uniform. Thirty-three species were found to have undulate to sinuous anticlinal cell walls [e.g. *Quercus stenophylloides* (Fig. 154), *Quercus glabricupula* (Fig. 179) *Quercus hondae* (Fig. 180), *Quercus gemelliflora* (*Kochummen, K.M. 40670*) (Fig. 181), *Quercus austrocochinchinensis* (Fig. 187), *Quercus gomeziana* (Fig. 188), *Quercus rex*

Table 3. Leaf epidermal features of *Quercus* subgenus *Cyclobalanopsis* in the present study

		Adaxial		Abaxial				Wax flake		Trichome types											Trichome base		
No.	Scientific name	Ep wall	Trichome base	Ep wall	Thick on epidermus	Stomata types	Stomata size (L × W) (μm)	Sm	Pl	F	SF	St	Ro	S	SSt	ALA	U	BU	Ca	P	U-STB	STB	CTB
1	*Quercus albicaulis*	str	STB	str	–	cyc	27.10 ± 1.45 × 22.06 ± 0.99	+	–	–	–	–	–	–	–	–	–	+	–	–	+	–	–
2	*Quercus annulata*	str-cur	STB	str-cur-un	–	cyc	23.62 ± 0.79 × 18.73 ± 0.68	–	+	–	–	–	–	–	–	+	+	–	–	–	+	+	–
3	*Quercus arbutifolia**	str-cur	STB	str	–/gl +(0&1)	cyc/an	22.31 ± 0.96 × 17.82 ± 0.6	–	+(1)	–(0)	–(0)	–(0)	–(0)	–(0)	+(1)	+(1)	+(1)	–(0)	–(0)	–(0)	+(1)	+(1)	–(0)
4	*Quercus argentata*	str-cur	STB	str	–	cyc	26.31 ± 1.61 × 21.04 ± 1.30	+	–	–	–	–	–	–	–	–	–	+	–	–	+	–	–
5	*Quercus argyrotricha*	str	STB	str	–	an	22.14 ± 0.87 × 18.92 ± 0.64	–	+	+	–	–	–	–	+	–	+	–	–	–	+	+	–
6	*Quercus asymmetrica*	str	STB	cur-ro	–	cyc	22.44 ± 1.26 × 19.01 ± 1.44	+	–	–	–	–	–	–	+	+	+	–	–	–	+	+	–
7	*Quercus asymmetrica*	str-cur	STB	str-cur-ro	–	cyc	19.62 ± 0.92 × 16.2 ± 0.46	+	–	–	–	–	–	–	+	+	+	–	–	–	+	+	–
8	*Quercus augustinii**	str	STB	str	–(0)	an	23.34 ± 1.19 × 16.53 ± 0.47	–	+(1)	–(0)	–(0)	–(0)	–(0)	–(0)	–(0)	–(0)	–	+(1)	–(0)	–(0)	+(1)	–(0)	–(0)
9	*Quercus auricoma*	str-cur	STB	str-cur	pa+	cyc	14.76 ± 0.99 × 13.23 ± 1.07	–	+	–	–	–	–	–	–	–	+	–	–	–	+	+	–
10	*Quercus austrocochinchinensis**	str-cur	STB/CTB	sin	–(0)	cyc	20.98 ± 1.19 × 17.81 ± 0.62	+(0)	–	–(0)	+(1)	–(0)	–(0)	–(0)	–(0)	–(0)	+(1)	–(0)	–(0)	–(0)	+(1)	–(0)	+(1)
11	*Quercus austroglauca*	str	STB	str	–	cyc/an	23.09 ± 1.00 × 16.82 ± 0.59	–	+	–	–	–	–	–	–	+	+	–	–	–	+	+	–
12	*Quercus bella*	str-cur	STB	str-cur	gl+	cyc	16.32 ± 0.53 × 14.68 ± 0.63	–	+	–	–	–	–	–	–	–	+	–	–	–	+	–	–
13	*Quercus blakei*	str-cur	STB	str-cur	–	cyc	19.94 ± 0.77 × 16.69 ± 0.47	+	–	–	–	–	–	–	–	–	+	–	–	–	+	+	–
14	*Quercus braianensis*	str	STB/CTB	str-cur	–	cyc	25.89 ± 1.46 × 19.89 ± 1.26	+	–	–	–	–	+	–	–	–	+	–	–	–	+	–	+
15	*Quercus brandisiana*	str-cur	STB	cur-ro	gl+	cyc	21.84 ± 1.12 × 17.32 ± 0.53	+	–	+	–	–	–	–	–	–	+	–	–	–	+	+	–
16	*Quercus brevicalyx*	str-cur	STB	str-cur	gl+	cyc/an	22.85 ± 1.56 × 19.00 ± 0.62	–	+	–	–	–	–	–	–	–	+	–	–	–	+	+	–
17	*Quercus brevicalyx*	str-cur	STB	cur-un	gl+	cyc	21.37 ± 1.02 × 18.19 ± 0.72	–	+	–	–	–	–	–	–	–	+	–	–	–	+	+	–
18	*Quercus championii**	str	STB/CTB	cur-un	–(0)	cyc	18.98 ± 0.63 × 15.02 ± 0.99	+(0)	–	–(0)	(0)	+(1)	–(0)	–(0)	–(0)	–(0)	+(1)	–(0)	–(0)	–(0)	+(1)	–(0)	+(1)
19	*Quercus chapensis*	un-sin	STB	str-cur	pa+	cyc	17.61 ± 0.85 × 14.83 ± 0.64	–	+	–	–	–	–	–	–	+	+	–	–	–	+	+	–
20	*Quercus chrysotricha*	str-cur	STB	cur-ro	gl+	cyc	23.64 ± 0.88 × 19.66 ± 0.36	–	+	–	–	–	–	–	–	–	+	–	–	–	+	+	–
21	*Quercus chrysotricha*	str	STB	cur-ro	gl+	cyc	27.15 ± 1.42 × 22.49 ± 1.16	–	+	–	–	–	–	–	–	–	+	–	–	–	+	+	–
22	*Quercus chungii*	str-cur	STB/CTB	cur-ro-un	–	cyc	21.95 ± 0.71 × 17.58 ± 0.61	–	+	–	–	+	–	–	–	–	+	–	–	–	+	–	+
23	*Quercus daimingshanensis*	str-cur	STB	cur-ro	gl+	cyc	22.05 ± 0.41 × 20.29 ± 0.74	–	+	–	–	–	–	–	–	–	+	–	–	–	+	+	–
24	*Quercus delavayi**	str-cur	STB/CTB	str-cur-ro	–(0)	cyc	19.15 ± 0.33 × 14.12 ± 0.66	+(0)	–	–(0)	–(0)	+(1)	–(0)	–(0)	–(0)	–(0)	+(1)	–(0)	–(0)	–(0)	+(1)	–(0)	+(1)
25	*Quercus disciformis*	str-cur	STB	un-sin	–	cyc	22.65 ± 0.86 × 19.19 ± 0.44	+	–	–	–	–	–	–	–	–	+	–	–	–	+	+	–
26	*Quercus edithae*	str-cur	STB	str-cur	–	cyc	23.07 ± 0.85 × 17.77 ± 0.54	+	–	–	–	–	–	–	–	+	+	–	–	–	+	+	–
27	*Quercus edithae**	cur-un-sin	STB	str-cur-sin	–(0)	cyc	24.12 ± 0.67 × 18.66 ± 0.35	+(0)	–	–(0)	–(0)	–(0)	–(0)	–(0)	–(0)	–(0)	+(1)	–(0)	–(0)	–(0)	+(1)	+(1)	–(0)
28	*Quercus elmeri*	str-cur	STB	str-cur	pa+	cyc/an	21.29 ± 0.61 × 17.70 ± 0.46	–	+	–	–	–	–	–	–	–	+	–	–	–	+	+	–
29	*Quercus gaharuensis*	str-cur	STB	str-cur	pa/gl+	cyc	27.10 ± 1.62 × 19.37 ± 0.75	–	+	–	–	–	–	–	–	–	+	–	–	–	+	+	–
30	*Quercus gambleana*	str	STB	str-cur	–	cyc	20.10 ± 0.62 × 17.92 ± 0.46	–	+	+	–	–	–	–	+	+	+	–	–	–	+	+	–
31	*Quercus gemelliflora*	str-cur	STB	str-cur	pa/gl+	cyc	23.34 ± 1.33 × 18.89 ± 1.57	–	+	–	–	–	–	–	–	–	+	–	–	–	+	+	–
32	*Quercus gemelliflora*	sin	STB	un-sin	–	cyc	23.57 ± 0.95 × 17.91 ± 0.51	+	–	–	–	–	–	–	–	–	+	–	–	–	+	+	–
33	*Quercus gilva*	cur-un	STB/CTB	str-cur	–	cyc	22.85 ± 1.41 × 17.44 ± 0.91	+	–	–	–	+	–	–	–	–	+	–	–	–	+	–	+
34	*Quercus glabricupula*	un-sin	STB	un-sin	–	cyc	21.46 ± 1.12 × 18.72 ± 0.60	–	+	–	–	–	–	–	–	+	+	–	–	–	+	+	–
35	*Quercus glauca**	str-cur	STB	str-cur	–(0)	cyc	28.11 ± 1.25 × 21.10 ± 0.70	–	+(1)	–(0)	–(0)	–(0)	–(0)	–(0)	–(0)	+(1)	+(1)	–(0)	–(0)	–(0)	+(1)	+(1)	–(0)
36	*Quercus glauca* f. *gracilis*	str-cur	STB	str-cur	–	cyc	20.61 ± 0.82 × 16.47 ± 0.24	–	+	–	–	–	–	–	–	+	+	–	–	–	+	+	–
37	*Quercus gomeziana*	str	STB/CTB	str-cur-un	–	cyc	22.86 ± 0.82 × 19.07 ± 0.44	+	–	–	+	–	–	–	–	–	+	–	–	–	+	–	+
38	*Quercus gomeziana*	str	STB/CTB	str-cur-un	–	cyc	18.91 ± 0.93 × 15.60 ± 0.55	+	–	–	+	–	–	–	–	–	+	–	–	–	+	–	+
39	*Quercus helferiana*	str	STB/CTB	cur-ro	–	cyc	20.97 ± 1.30 × 18.04 ± 1.22	+	–	–	+	–	–	–	–	–	+	–	–	–	+	–	+
40	*Quercus hondae*	un-sin	STB	un-sin	–	cyc	23.81 ± 1.34 × 21.63 ± 0.94	+	–	–	–	–	–	–	–	–	+	–	–	–	+	+	–
41	*Quercus hypargyrea*	str	STB	str-cur	–	cyc	23.05 ± 0.85 × 17.20 ± 0.45	–	+	–	–	–	–	–	–	+	–	–	–	–	–	+	–
42	*Quercus jenseniana**	str-cur	STB	str-cur	gl+(1)	cyc	23.44 ± 1.26 × 16.33 ± 0.66	–	+(1)	–(0)	–(0)	–(0)	–(0)	–(0)	–(0)	–(0)	–(0)	+(1)	–(0)	–(0)	+(1)	–(0)	–(0)
43	*Quercus kerangasensis*	str-cur	STB	cur-ro	gl+	cyc	22.78 ± 1.83 × 20.21 ± 1.90	–	+	–	–	–	–	–	–	+	+	–	–	–	+	+	–
44	*Quercus kerrii**	str-cur	STB/CTB	cur-ro	–(0)	cyc	19.38 ± 0.50 × 14.54 ± 0.58	+(0)	–	–(0)	+(1)	–(0)	–(0)	–(0)	–(0)	–(0)	+(1)	–(0)	–(0)	–(0)	+(1)	–(0)	+(1)
45	*Quercus kinabaluensis*	str-cur	STB	cur-ro	–	cyc	20.65 ± 1.46 × 17.88 ± 0.72	–	+	–	–	–	–	–	–	+	–	–	–	–	–	+	–
46	*Quercus kiukiangensis*	str-cur	STB	str-cur	pa+	cyc	24.58 ± 1.35 × 20.69 ± 0.96	–	+	–	–	–	–	–	–	+	+	–	–	–	+	+	–
47	*Quercus kouangsiensis*	str-cur	STB	str-cur	pa/gl+	cyc	16.30 ± 0.79 × 15.06 ± 0.62	–	+	–	–	–	–	–	–	–	?	–	–	–	+	+	–
48	*Quercus lamellosa*	str-cur	STB	cur-un	–	cyc	25.11 ± 0.72 × 21.74 ± 0.66	–	+	–	–	–	–	–	–	+	+	–	–	–	+	+	–
49	*Quercus lamellosa*	str-cur	STB	cur-un	–	cyc	23.91 ± 1.88 × 20.84 ± 1.56	–	+	–	–	–	–	–	–	+	+	–	–	–	+	+	–
50	*Quercus langbianensis**	str-cur	STB	str-cur	pa+(1)	cyc	17.30 ± 0.85 × 14.45 ± 0.77	–	+(1)	–(0)	–(0)	–(0)	–(0)	–(0)	–(0)	?	+(1)	–(0)	–(0)	–(0)	+(1)	+(1)	–(0)
51	*Quercus lineata*	str-cur	STB	str-cur-ro	gl+	cyc	23.91 ± 1.39 × 21.78 ± 1.28	–	+	–	–	–	–	–	–	+	+	–	–	–	+	+	–
52	*Quercus lineata*	str-cur	STB	str-cur-ro	gl+	cyc	24.23 ± 0.92 × 20.80 ± 0.52	–	+	–	–	–	–	–	–	+	+	–	–	–	+	+	–
53	*Quercus litseoides*	str-cur-un	STB	cur-un	–	cyc	22.82 ± 0.93 × 17.93 ± 0.55	–	+	–	–	–	–	–	–	–	+	–	–	–	+	+	–
54	*Quercus lobbii*	cur-un	STB/CTB	cur-un	–	cyc	27.17 ± 1.05 × 20.64 ± 1.25	+	–	–	–	+	–	–	–	–	+	–	–	–	+	–	+
55	*Quercus lobbii*	str-cur	STB/CTB	cur-un	–	cyc	27.38 ± 1.78 × 21.53 ± 0.66	+	–	–	–	+	–	–	–	–	+	–	–	–	+	–	+
56	*Quercus longistyla*	str-cur-un	STB	cur-un	–	cyc	23.86 ± 0.97 × 19.21 ± 0.65	–	+	–	–	–	–	–	–	–	+	–	–	–	+	+	–
57	*Quercus lowii*	str-cur	STB	cur-ro	–	cyc	29.92 ± 1.11 × 23.37 ± 1.39	–	+	–	–	–	–	–	+	–	–	–	–	–	–	+	–
58	*Quercus macrocalyx*	str-cur-un	STB	str-cur	gl/pa+	cyc	22.00 ± 0.90 × 15.34 ± 0.84	–	+	–	–	–	–	–	–	–	+	–	–	–	+	+	–
59	*Quercus merrillii*	str	STB	cur-ro	gl+	cyc	28.87 ± 0.98 × 23.47 ± 0.50	–	+	–	–	–	–	–	–	–	+	–	–	–	+	+	–
60	*Quercus mespilifolia*	str-cur	STB/CTB	str-cur	–	cyc	14.01 ± 0.45 × 11.36 ± 0.21	+	–	–	–	+	–	–	–	–	+	–	–	–	+	–	+

Table 3. *Continued*

		Adaxial		Abaxial				Wax flake		Trichome types											Trichome base		
No.	Scientific name	Ep wall	Trichome base	Ep wall	Thick on epidermus	Stomata types	Stomata size (L × W) (μm)	Sm	Pl	F	SF	St	Ro	S	SSt	ALA	U	BU	Ca	P	U-STB	STB	CTB
61	*Quercus mespilifolia*	str-cur	STB/CTB	str-cur	–	cyc	24.71 ± 1.24 × 20.87 ± 0.91	+	–	–	–	+	–	–	–	–	+	–	–	–	+	–	+
62	*Quercus miyagii*	str-cur	STB	str-cur-ro	–	cyc	27.27 ± 1.78 × 20.61 ± 0.88	–	+	–	–	–	–	–	–	–	+	–	–	–	+	+	–
63	*Quercus morii*	cur-un	STB	cur-sin	–	cyc	28.28 ± 1.45 × 24.94 ± 1.07	–	+	–	–	–	–	–	–	+	+	–	–	–	+	+	–
64	*Quercus motuoensis*	str-cur	STB	str-cur-ro	–	cyc	22.98 ± 0.74 × 21.91 ± 0.60	+	–	–	–	–	–	–	–	–	–	+	–	–	+	–	–
65	*Quercus myrsinifolia*	str-cur	STB	str-cur	–	cyc/an	22.65 ± 1.05 × 17.20 ± 0.45	–	+	–	–	–	–	–	–	+	+	–	–	–	+	+	–
66	*Quercus neglecta*	st-cur	STB	str-cur	–/gl+	cyc	21.65 ± 1.65 × 16.35 ± 1.46	–	+	–	–	–	–	–	–	–	+	–	–	–	+	–	–
67	*Quercus ninganensis*	str-cur	STB	str-cur	–	cyc	27.91 ± 1.45 × 20.60 ± 1.10	–	+	+	–	–	–	–	+	+	+	–	–	–	+	+	–
68	*Quercus nivea*	str-cur	STB	str-cur	–	cyc	28.46 ± 0.87 × 23.09 ± 0.57	–	+	–	–	–	–	–	+	–	+	–	–	–	+	+	–
69	*Quercus oidocarpa*	str	STB	str-cur	–	cyc	18.06 ± 0.85 × 14.20 ± 0.55	–	+	+	–	–	–	–	+	–	+	–	–	–	+	+	–
70	*Quercus oxyodon*	str	STB	str-cur-un	–	cyc/an	16.80 ± 1.52 × 13.63 ± 1.09	–	+	–	–	–	–	–	–	+	+	–	–	–	+	+	–
71	*Quercus pachyloma*	un	STB	str-cur	pa+	cyc	17.29 ± 0.90 × 14.55 ± 0.67	–	+	–	–	–	–	–	–	–	+	–	–	–	+	–	–
72	*Quercus percoriacea*	str	STB	str-cur	–	cyc/an	22.40 ± 1.47 × 16.60 ± 0.58	–	+	–	–	–	–	–	+	+	+	–	–	–	+	+	–
73	*Quercus phanera*	str-cur	STB	cur-ro	–	cyc	22.85 ± 0.76 × 19.69 ± 0.30	+	–	–	–	–	–	–	–	–	+	–	–	–	+	–	–
74	*Quercus pseudoverticillata*	str-cur	STB	cur-ro	gl+	cyc	18.17 ± 0.88 × 15.58 ± 0.98	–	+	–	–	–	–	–	–	–	–	+	–	–	+	–	–
75	*Quercus quangtriensis*	un-sin	STB	str-cur-un	pa+	cyc/an	18.63 ± 0.70 × 15.61 ± 0.63	–	+	–	–	–	–	–	–	–	–	–	–	–	–	+	–
76	*Quercus ramsbottomii*	str-cur	STB	str-cur	pa/gl+	cyc	17.36 ± 0.60 × 14.85 ± 0.27	–	+	–	–	–	–	–	–	–	+	–	–	–	+	+	–
77	*Quercus rex**	cur-un	STB/CTB	cur-un	pa+(1)	cyc/an	15.21 ± 0.47 × 14.26 ± 0.50	+(0)	–	–(0)	+(1)	–(0)	–(0)	–(0)	–(0)	–(0)	+(1)	–(0)	–(0)	–(0)	+(1)	–(0)	+(1)
78	*Quercus rupestris*	str	STB	cur-ro	–	cyc	24.02 ± 0.59 × 21.08 ± 0.28	+	–	–	–	–	–	–	–	–	+	–	–	–	+	+	–
79	*Quercus salicina*	str	STB	str-cur	–	cyc/an	21.39 ± 1.13 × 16.92 ± 1.06	–	+	–	–	–	–	–	+	+	+	–	–	–	+	+	–
80	*Quercus salicina**	str-cur	STB	str-cur	–(0)	cyc/an	18.62 ± 0.54 × 15.68 ± 0.76	–	+(1)	+(1)	–(0)	–(0)	–(0)	+(1)	+(1)	–(0)	+(1)	–(0)	–(0)	–(0)	+(1)	+(1)	–(0)
81	*Quercus schottkyana*	str	STB	str-cur	–	cyc	15.44 ± 0.73 × 11.45 ± 0.39	–	+	–	–	–	–	–	–	+	+	–	–	–	+	+	–
82	*Quercus semiserrata*	un-sin	STB	cur-sin	pa+	cyc/an	16.45 ± 0.57 × 13.94 ± 0.26	–	+	–	–	–	–	–	–	–	+	–	–	–	+	+	–
83	*Quercus sessilifolia*	str-cur	STB	str-cur	–	cyc	24.37 ± 1.09 × 19.79 ± 0.62	–	+	–	–	–	–	–	–	+	+	–	–	–	+	+	–
84	*Quercus sichourensis**	str-cur	STB/CTB	un-sin	–(0)	an	22.50 ± 0.86 × 16.92 ± 0.60	+(0)	–	–(0)	–(0)	+(1)	+(1)	–(0)	–(0)	–(0)	+(1)	–(0)	–(0)	–(0)	+(1)	–(0)	+(1)
85	*Quercus steenisii*	cur-ro	STB	str-cur	–	cyc	19.07 ± 0.59 × 16.56 ± 0.46	+	–	+	–	–	–	–	–	–	+	–	–	–	+	+	–
86	*Quercus stenophylloides*	str-cur	STB	un-sin	–	cyc	20.23 ± 1.04 × 12.45 ± 0.39	–	+	–	–	–	–	–	–	+	–	–	–	–	–	+	–
87	*Quercus stewardiana*	str-cur	STB	cur-ro	gl+	cyc	18.70 ± 0.86 × 17.08 ± 1.30	–	+	–	–	–	–	–	–	+	+	–	–	–	+	+	–
88	*Quercus stewardiana*	str-cur	STB	cur-ro	pa+	cyc	19.79 ± 0.60 × 15.82 ± 0.36	–	+	–	–	–	–	–	–	+	+	–	–	–	+	+	–
89	*Quercus subsericea*	str-cur	STB	str-cur-un	–	cyc	24.31 ± 1.25 × 15.35 ± 0.67	–	+	–	–	–	–	–	+	+	+	–	–	–	+	+	–
90	*Quercus sumatrana*	str	STB	str	–	cyc	20.23 ± 1.14 × 16.30 ± 0.59	–	+	–	–	–	–	–	–	+	+	–	–	–	+	+	–
91	*Quercus tenuicupula*	str-cur	STB	str-cur-un	–	cyc	20.20 ± 0.64 × 16.05 ± 0.26	–	+	–	–	–	–	–	–	–	–	+	–	–	+	–	–
92	*Quercus thomsoniana*	str	STB	str-cur	–	an	17.05 ± 0.84 × 15.26 ± 0.58	–	+	–	–	–	–	–	–	+	+	–	–	–	+	+	–
93	*Quercus thorelii*	str	STB/CTB	un-sin	–	cyc	19.48 ± 1.01 × 17.18 ± 0.91	+	–	–	+	–	–	–	–	–	+	–	–	–	+	–	+
94	*Quercus tiaoloshanica*	str-cur	STB	cur-ro	gl+	cyc	23.65 ± 0.51 × 18.37 ± 0.51	+	–	–	–	–	–	–	–	–	+	–	–	–	+	–	–
95	*Quercus tomentosinervis*	str-cur	STB	str-cur	gl ±	cyc/an	25.70 ± 1.52 × 24.17 ± 1.08	–	+	–	–	–	–	–	–	–	–	+	–	–	+	–	–
96	*Quercus tranninhensis*	str-cur	STB	str-cur	–	cyc	19.44 ± 1.19 × 15.09 ± 0.75	–	+	–	–	–	–	–	–	+	+	–	–	–	+	+	–
97	*Quercus treubiana*	str	STB	str-cur	gl+	cyc	19.63 ± 1.29 × 16.26 ± 0.61	–	+	–	–	–	–	–	–	–	+	–	–	–	+	+	–
98	*Quercus treubiana*	str	STB	str-cur	gl+	cyc	17.75 ± 0.86 × 14.88 ± 0.76	–	+	–	–	–	–	–	–	–	+	–	–	–	+	+	–
99	*Quercus valdinervosa*	str	STB	str-cur-ro	pa/gl+	cyc	20.09 ± 1.21 × 15.4 ± 0.68	–	+	–	–	–	–	–	–	–	+	–	–	–	+	+	–
100	*Quercus wangsaiensis*	un-sin	STB	cur-sin	–	cyc	19.71 ± 0.55 × 14.20 ± 0.42	–	+	–	–	–	–	–	–	+	+	–	–	–	+	+	–
101	*Quercus xanthotricha*	str-cur	STB	cur-un	–	cyc	25.07 ± 0.97 × 22.10 ± 0.91	–	+	–	–	–	–	–	–	+	–	–	–	–	–	+	–
102	*Quercus utilis*	NA	NA	cur-sin	–(0)	am/step	18–25 × 14–18	+(0)	–	–(0)	+(1)	–(0)	–(0)	–(0)	–(0)	–(0)	+(1)	–(0)	–(0)	–(0)	+(1)	–(0)	–(1)
103	*Quercus acrodonta*	NA	NA	cur	–(0)	am/step	21–25 × 16–23	+(0)	–	–(0)	–(0)	+(1)	–(0)	–(0)	–(0)	–(0)	?	–(0)	+(1)	–(0)	+(1)	–(0)	+(1)
104	*Quercus aquifolioides*	NA	NA	un	–(0)	am/sten/ cyc	23–30 × 23–30	+(0)	–	–(0)	–(0)	+(1)	–(0)	–(0)	–(0)	–(0)	+(1)	+(1)	–(0)	–(0)	+(1)	–(0)	+(1)
105	*Castanopsis indica*	str	STB	cur-sin	–(0)	cyc	NA	+(0)	–	+(1)	–(0)	–(0)	–(0)	–(0)	–(0)	–(0)	+(1)	–(0)	–(0)	+(1)	+(0)	+(1)	–(0)

*Selected leaf epidermal features were scored and traced on the ITS tree of Deng *et al*. (2013b).
Data for No. 102 and 103 were obtained from Zhou *et al*. (1995); data for No. 104 were obtained from Zhou *et al*. (1995) and Yang *et al*. (2012). Data for No. 105 were obtained from Liu *et al*. (2009).
+, present; –, absent.
Ep wall (epidermal cell wall pattern): straight (str); curved (cur); undulate (un); sinuous (sin).
Trichome base: single-celled trichome base (STB); compound trichome base (CTB).
Thick on ep (thickening on epidermal cells): papillae (pa); globular (gl); flat (–).
Stomata types: anomocytic (an); cyclocytic (cyc), stephanocytic (step).
Wax flake: Sm (smooth); Pl (platelet).
Trichome types: F (fasciculate); SF (stipitate fasciculate); St (stellate); Ro (rosulate); S (solitary); SSt (simple stellate); ALA (appressed lateral attached); U (uniseriate); BU (branched uniseriate); Ca (capitate). P (peltate).
U-STB (single-celled trichome base of thin-walled trichomes, transparent to semi-transparent); STB (single-celled trichome base of unicelluar thick-walled trichomes, small, the cell wall dark stained); CTB (compound trichome base). Scored character states of wax flake, trichome types and trichome base: present (1); absent (0). NA: not available.

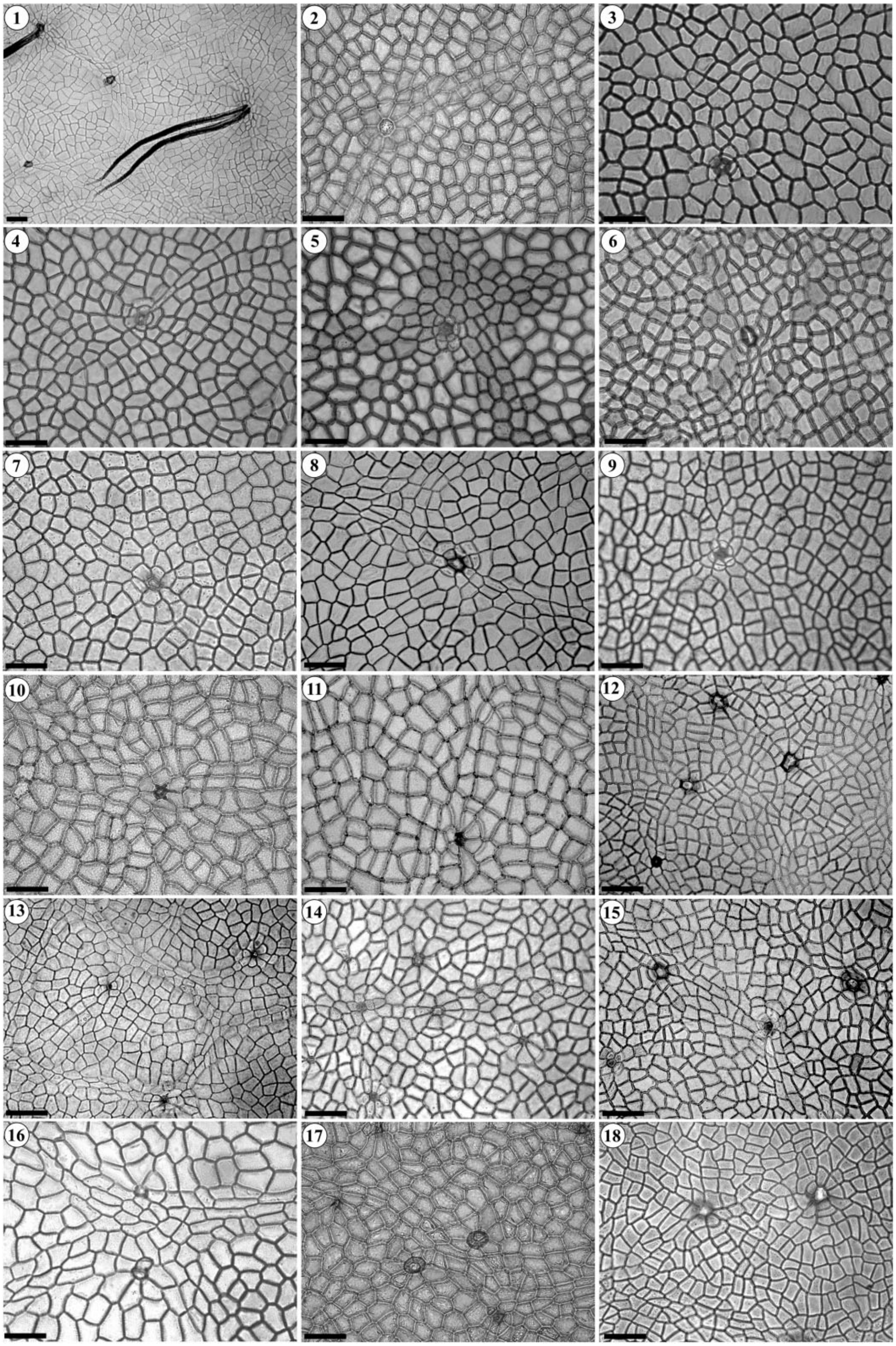

Figure 1–18. Light microscopy of leaf adaxial epidermis, showing straight to curved anticlinal wall; scale bar = 50 μm. 1. Q. salicina (Deng, M *et al*. 4727); 2. *Quercus albicaulis*; 3. *Quercus glauca*; 4. *Quercus subsericea*; 5. *Quercus rupestris*; 6. *Quercus percoriacea*; 7. *Quercus miyagii*; 8. *Quercus oidocarpa*; 9. *Quercus stenophylloides*; 10. *Quercus chrysotricha*; 11. *Quercus gemelliflora* (Medan 45417); 12. *Quercus thomsoniana*; 13. *Quercus sumatrana*; 14. *Quercus lineata* (Chew, W.L. 804); 15. *Quercus valdinervosa*; 16. *Quercus tranninhensis*; 17. *Quercus treubiana* (Kostermans, S.A. 7442); 18. *Quercus augustinii*.

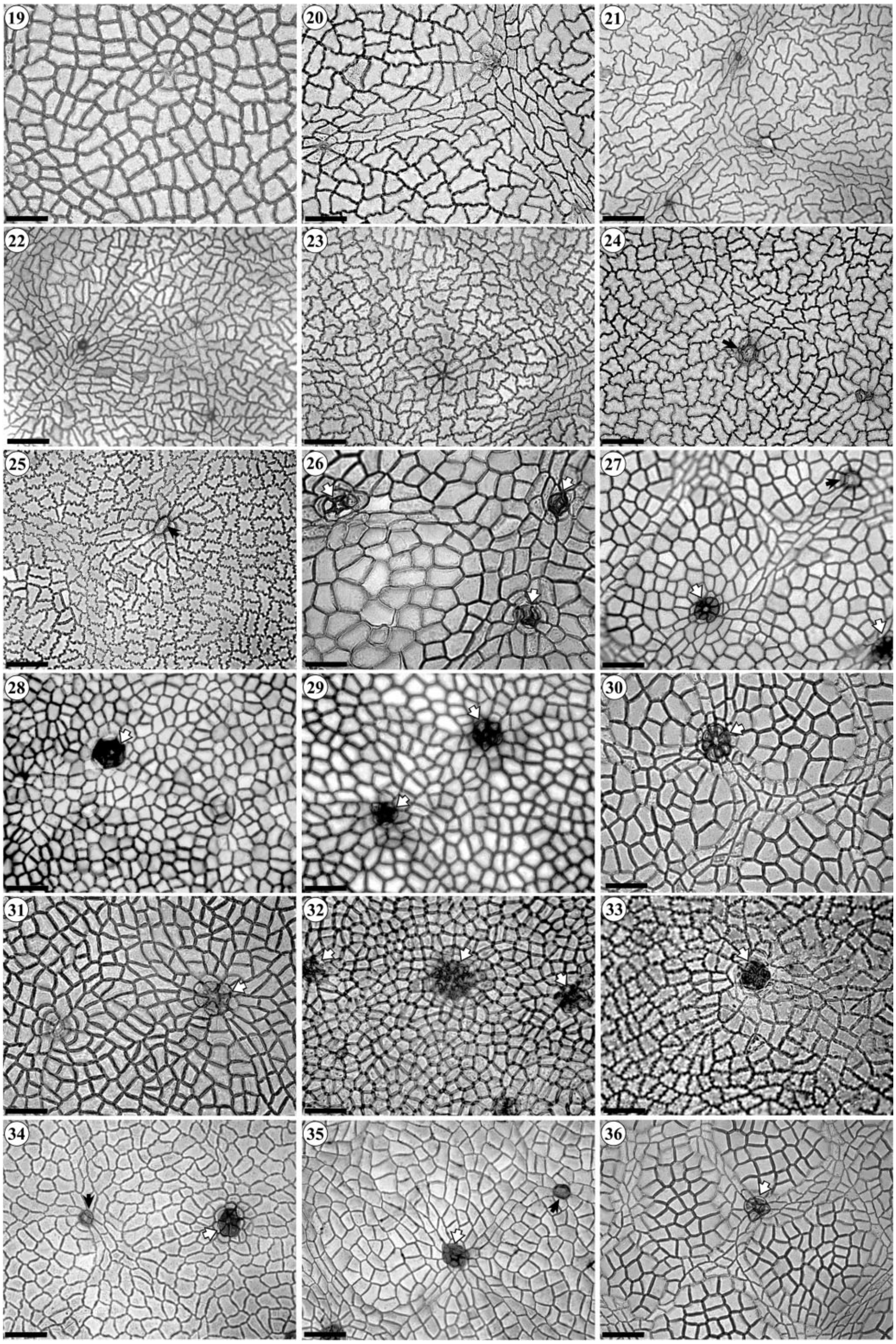

Figure 19–36. Light microscopy of leaf adaxial epidermis. 19–25. Showing undulate to sinuous anticlinal wall; 26–36. Showing compound trichome base (CTB). The white arrow shows CTB, the black arrow shows single-celled trichome base (STB); scale bar = 50 µm. 19. *Quercus edithae* (Maung Mya, 5359); 20. *Quercus glabricupula*; 21. *Quercus chapensis*; 22. *Quercus semiserrata*; 23. *Quercus quangtriensis*; 24. *Quercus gemelliflora* (Kochummen, K.M. 40670); 25. *Quercus hondae*; 26. *Quercus mespilifolia* (Wallich, N. 2766); 27. *Quercus austrocochinchinensis*; 28. *Quercus helferiana*; 29. *Quercus kerrii*; 30. *Quercus gomeziana* (Brandis, D. 530); 31. *Quercus lobbii* (Clarke, C.B. 15451); 32. *Quercus braianensis*; 33. *Quercus delavayi*; 34. *Quercus gilva*; 35. *Quercus sichourensis*; 36. *Quercus thorelii*.

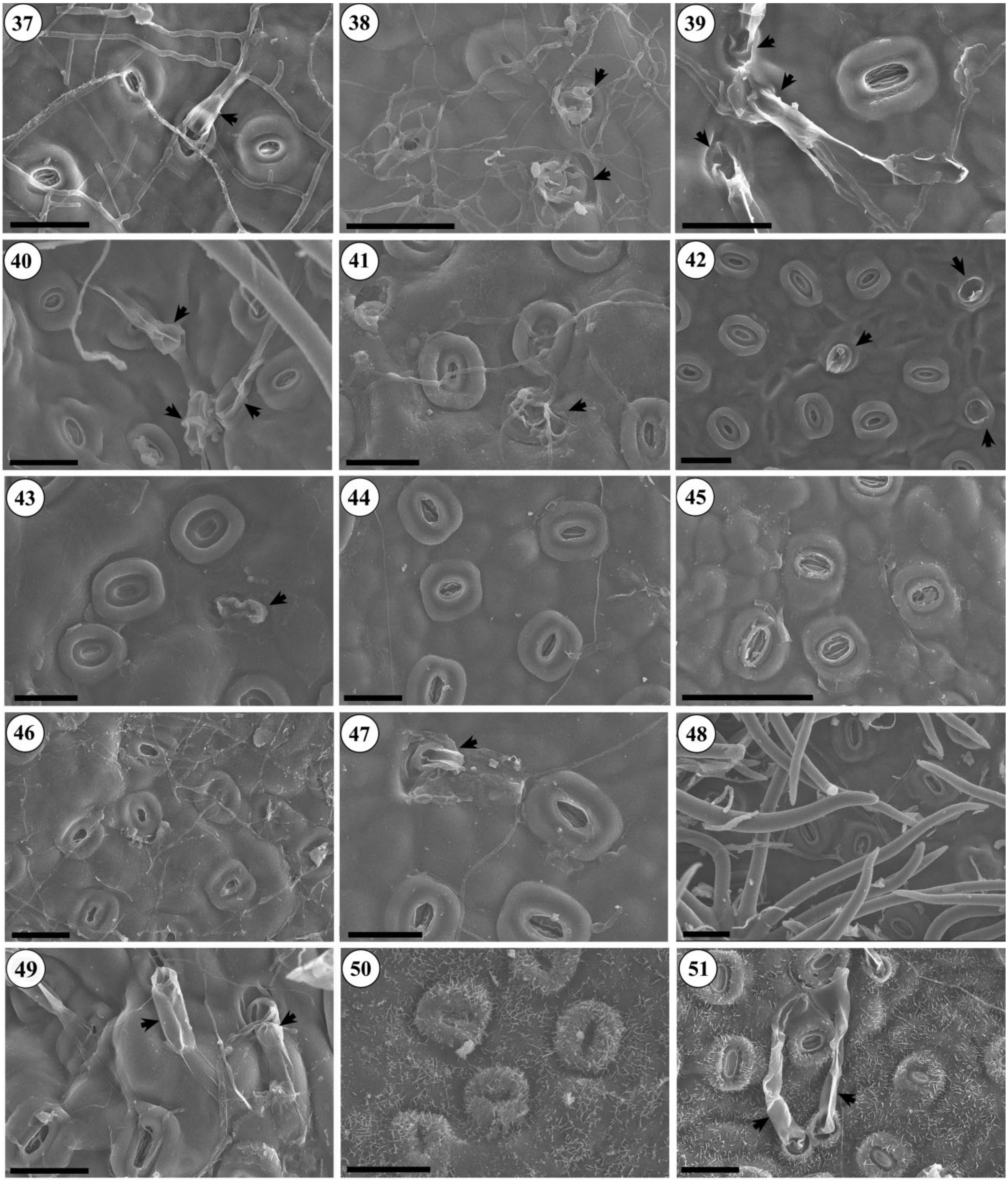

Figure 37–51. Scanning electron microscopy of leaf abaxial epidermis. 37–49. Showing the smooth wax flake; 50–51. Showing extremly small and thin platelet wax flake, black arrows showing thin-walled trichomes; scale bar = 20 μm. 37. *Quercus thorelii*; 38. *Quercus gomeziana* (King 3405); 39. *Quercus austrocochinchinensis*; 40. *Quercus kerrii*; 41. *Quercus albicaulis*; 42. *Quercus argentata*; 43. *Quercus rupestris*; 44. *Quercus edithae* (Deng, M *et al*. 4322); 45. *Quercus motuoensis*; 46. *Quercus disciformis*; 47. *Quercus hondae*; 48. *Quercus mespilifolia* (Alan, 10284); 49.*Quercus blakei*; 50. *Quercus longistyla*; 51. *Quercus helferiana*.

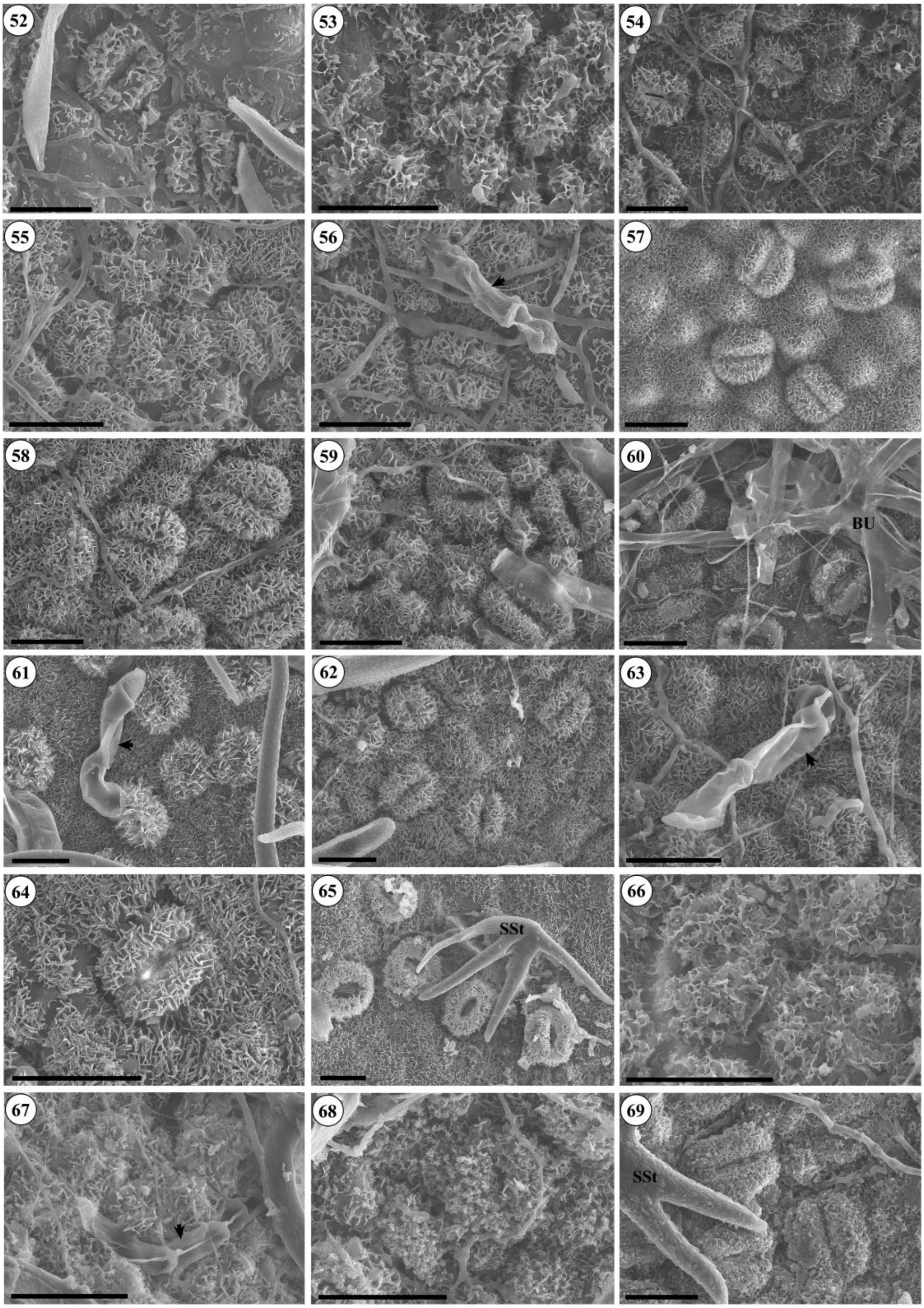

Figure 52–69. Scanning electron microscopy of leaf abaxial epidermis, showing platelet wax flake and trichomes. Black arrowing shows Uniseriate (U), simplified stellate trichomes (SSt); scale bar = 20 μm. 52. *Quercus lowii*; 53. *Quercus brevicalyx* (Kerr, A.F.G. 21017); 54. *Quercus chrysotricha* (Chai, P. 35492); 55. *Quercus oidocarpa*; 56. *Quercus percoriacea*; 57. *Quercus neglecta*; 58. *Quercus augustinii*; 59. *Quercus jenseniana*; 60. *Quercus tenuicupula*; 61. *Quercus salicina* (Deng, M *et al*. 4727); 62. *Quercus glauca*; 63. *Quercus annulata*; 64. *Quercus lamellosa* (Deng, M *et al*. 3736); 65. *Quercus subsericea*; 66. *Quercus nivea*; 67. *Quercus lineata* (Chew, W.L. 804); 68. *Quercus thomsoniana*; 69. *Quercus arbutifolia*.

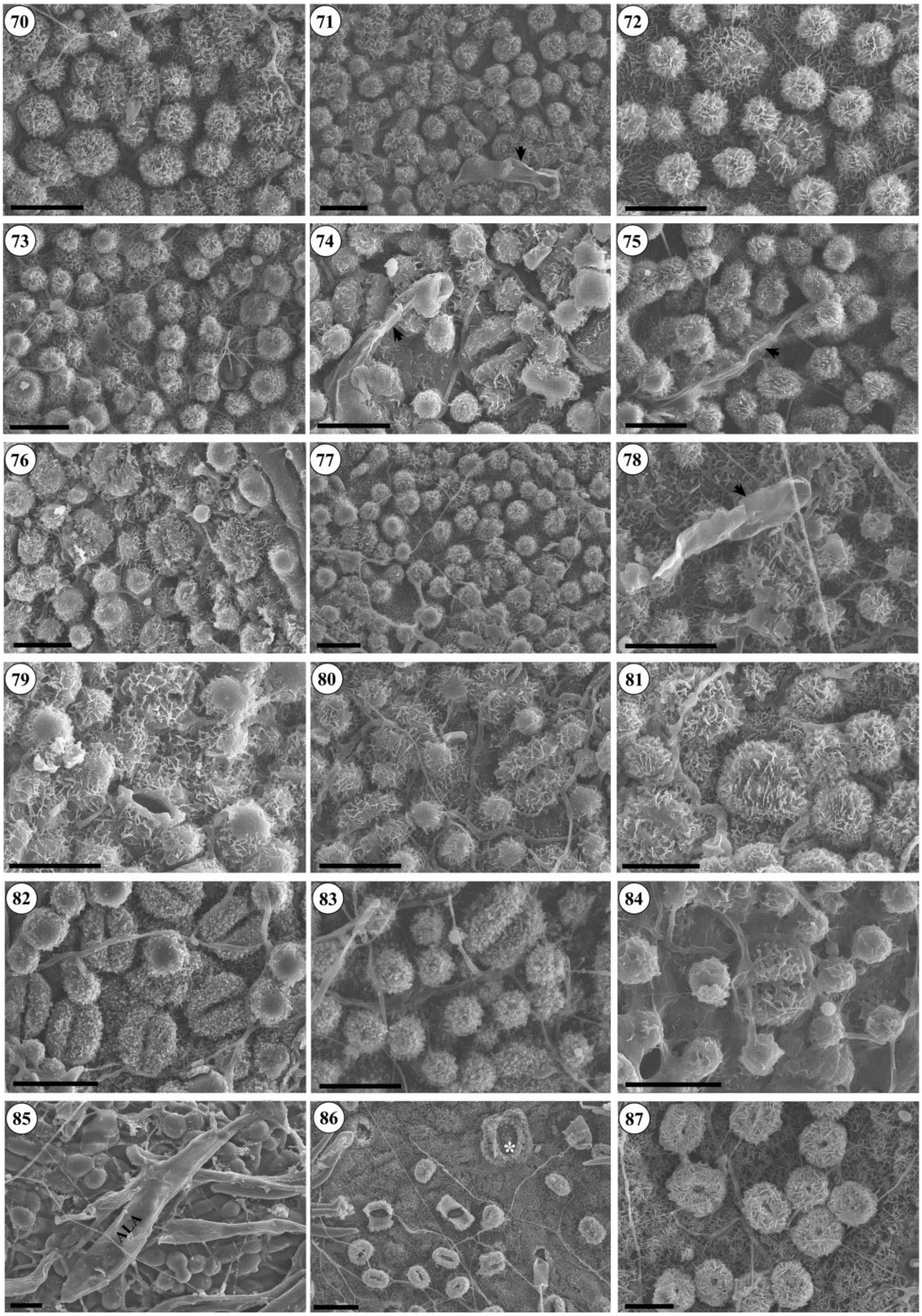

Figure 70–87. Scanning electron microscopy of leaf abaxial epidermis, black arrow shows U, appressed laterally attached trichome (ALA); scale bar = 20 µm. 70–85. Showing the papillae on epidermal cells, 86–87. Stomatal wax chimoney. 70. *Quercus ramsbottomii*; 71. *Quercus langbianensis*; 72. *Quercus pachyloma*; 73. *Quercus auricoma*; 74. *Quercus gaharuensis*; 75. *Quercus elmeri*; 76. *Quercus gemelliflora* (Medan, 45417); 77. *Quercus kouangsiensis*; 78. *Quercus chapensis*; 79. *Quercus treubiana* (Hallier, J.G. 2915); 80. *Quercus bella*; 81. *Quercus damingshanensis*; 82. *Quercus arbutifolia*; 83. *Quercus stewardiana* (Deng, M. 3780); 84. *Quercus quangtriensis*; 85. *Quercus pseudoverticillata*; 86. *Quercus chungii*, '*' indicating the extremly large stomata; 87. *Quercus xanthotricha*.

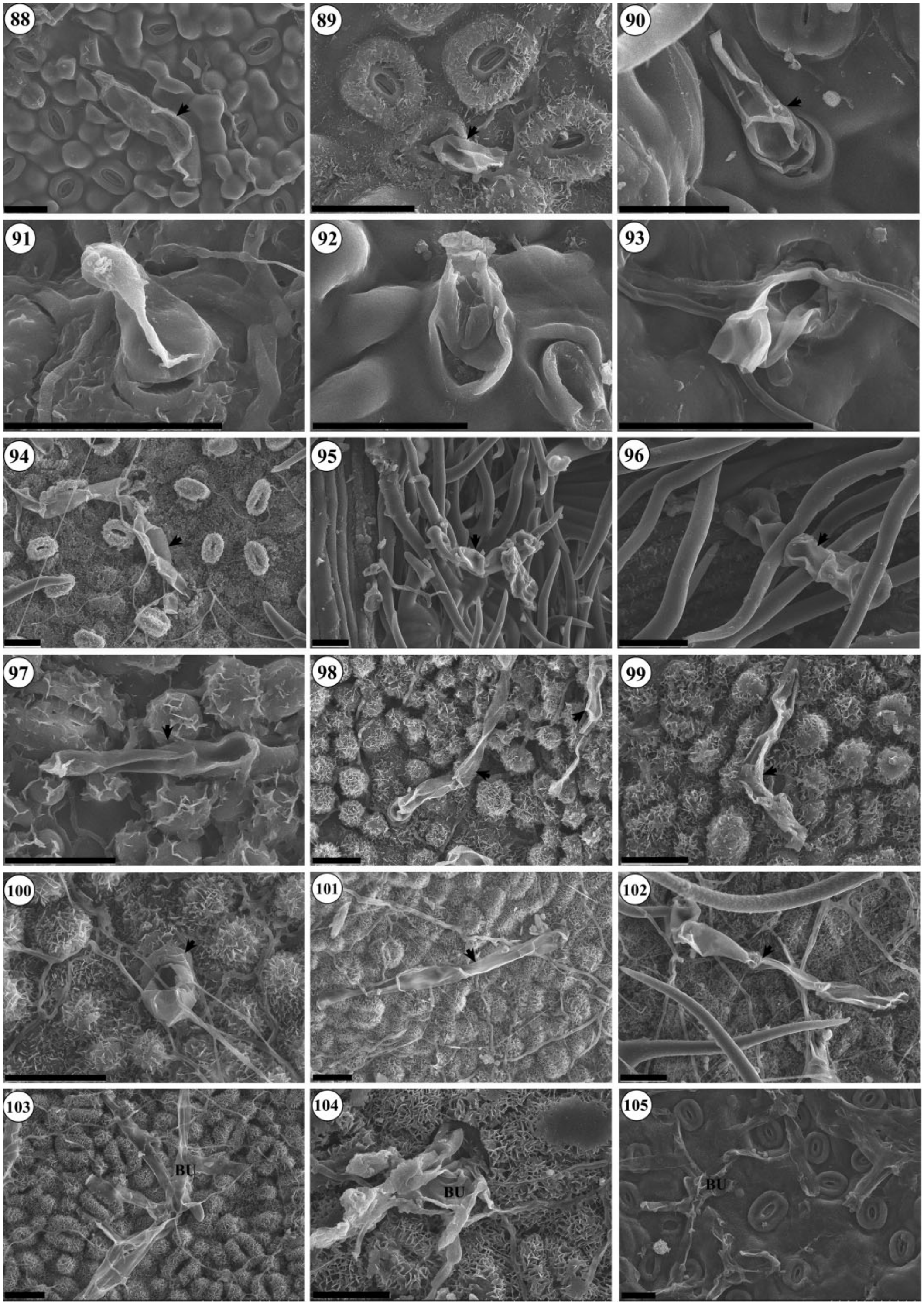

Figure 88–105. Scanning electron microscopy of leaf abaxial epidermis, showing thin-walled trichomes. 88–102. Simple Uniseriate (shown by black arrow), 103–105. Branched uniseriate (BU); scale bar = 20 μm. 88. *Quercus brandisiana*; 89. *Quercus mespilifolia* (Wallich, N. 2766); 90. *Quercus kerrii*; 91. *Quercus nivea*; 92. *Quercus brevicalyx* (Yang, S.R. 9); 93. *Quercus phanera*; 94. *Quercus chungii*; 95. *Quercus championii*; 96. *Quercus delavayi*; 97. *Quercus valdinervosa* (Chai, P.S. 35849); 98. *Quercus gaharuensis*; 99. *Quercus brevicalyx* (Kerrt, A.T.G. 21017); 100. *Quercus treubiana* (Kostermans, S.A. 7442); 101. *Quercus oxyodon*; 102. *Quercus ninganensis*; 103. *Quercus jenseniana*; 104. *Quercus augustinii*; 105. *Quercus albicaulis*.

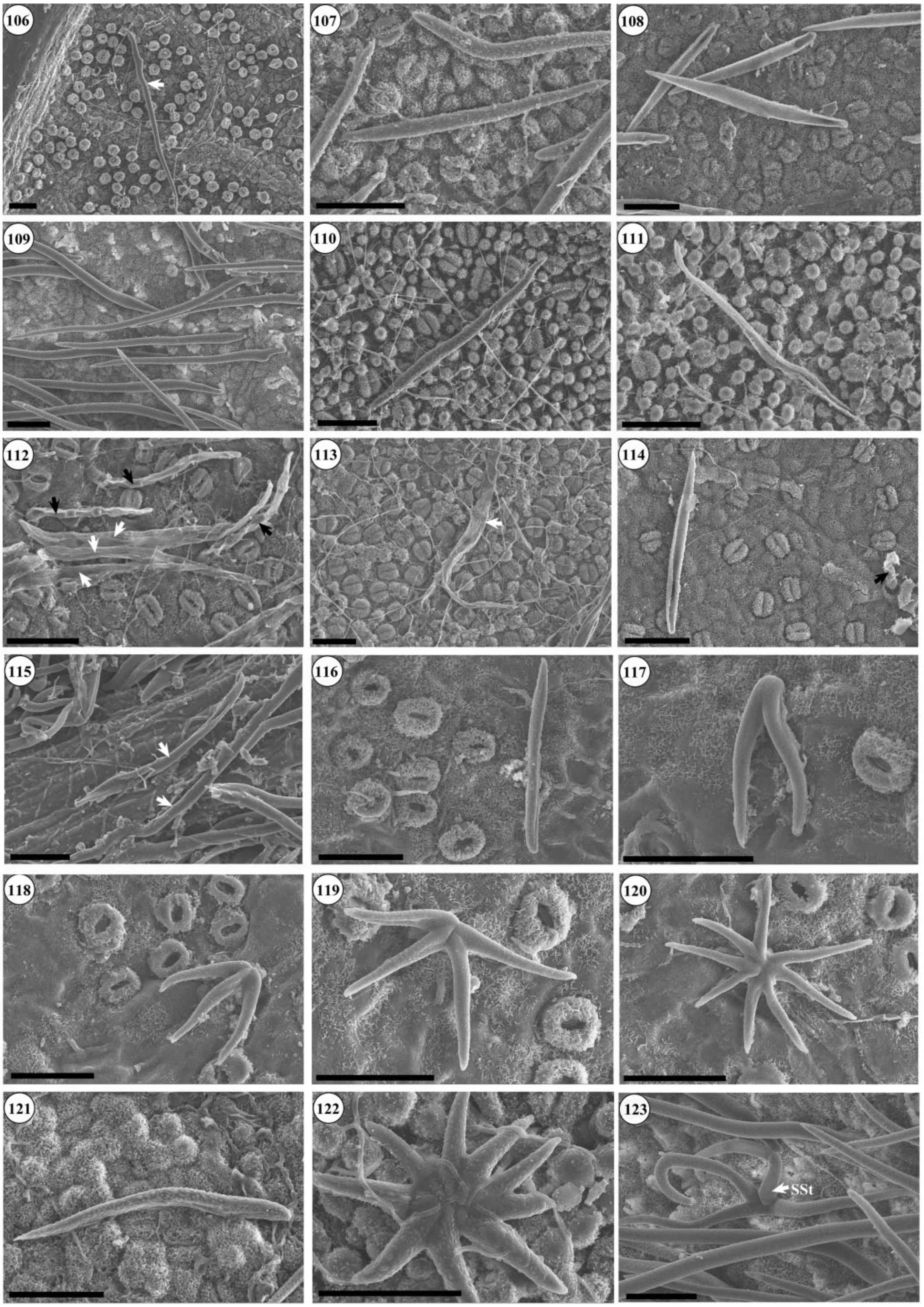

Figure 106–123. Scanning electron microscopy of Leaf abaxial epidermis, showing sppressed laterally attached trichome (ALA) (106–116 & 121) and SSt (117–120, 122 & 123), Black arrow indicates U; white arrow indicates ALA; scale bar = 50 μm. 106. *Quercus xanthotricha*; 107. *Quercus thomsoniana*; 108. *Quercus glauca*; 109. *Quercus salicina* (Deng, M *et al*. 3700); 110. *Quercus stewardiana*; 111. *Quercus kiukiangensis*; 112. *Quercus morii*; 113. *Quercus sumatrana*; 114. *Quercus lamellosa*; 115. *Quercus gambleana*; 116–120. *Quercus subsericea* (different views on the same slide, showing ALA and SSt with 2, 3, 4 and 8 arms); 121–122. *Quercus arbutifolia* (different views on the same slide, showing ALA and SSt); 123. *Quercus salicina* (Deng, M *et al*. 3700) (white arrow showing simiplified stellate trichome [SSt]).

(Fig. 194), and *Quercus sichourensis* (Figs 192, 195)]. Thirty-six specimens were found to have obvious globular to finger-like, convex papillae on their epidermal cells (Figs 70–85, 98, 99, 103, 110, 111, 166, 170, 173–178, 194).

Stomatal apparatus

Stomata were found only on the abaxial leaf surface of the leaves in subgenus *Cyclobalanopsis*. The guard cells were covered by the same kind of epicuticular wax as the other leaf epidermal cells. The aperture rim (outer stomatal ledge) of the stomata was usually raised above the epidermal cells with prominent, dark-stained thickenings, making the stomatal apparatus appear to be a ring or lip-like structure by LM (Figs 151–160, 163, 181, 183–195). The flat, slightly thickened aperture rim (outer stomatal ledge) is usually present in species with dense, stellate or stipitate, fasciculate trichomes [e.g. *Quercus gilva* (Fig. 184), *Quercus delavayi* (Fig. 185), *Quercus lobbii* (Fig. 186), *Q. austrocochinchinensis* (Fig. 187), *Q. gomeziana* (Fig. 188), and *Quercus thorelii* (Fig. 193)].

Following the terminology of Dilcher (1974), two main stomatal apparatus types were found in the present study:

1. Anomocytic stomata (Figs 153, 155, 156, 158, 170, 179–181): cells adjacent to the guard cells are not differentiated in any way from the normal epidermal cells.
2. Cyclocytic stomata (Figs 159, 163, 169, 179–181, 184, 187–190, 193): a single ring of small cells encloses the guard cells. This stomata type is common in subgenus *Cyclobalanopsis*. However, the cyclocytic stomata of most species of subgenus *Cyclobalanopsis* are not typical, since the rings formed by subsidiary cells are not distinct (e.g. Figs 151, 152, 158). Typical cyclocytic stomata are only found in a few species of subgenus *Cyclobalanopsis*: *Quercus disciformis* (Fig. 159), *Quercus albicaulis* (Fig. 163), *Quercus rupestris* (Fig. 169), *Q. glabricupula* (Fig. 179), *Q. hondae* (Fig. 180), and *Q. austrocochinchinensis* (Fig. 187). The stomata are usually aggregated in areoles. The subsidiary cells are shared by different stomata and are uniform in morphology, although the subsidiary cells of the stomata are usually stained a different colour than the other epidermal cells (Figs 151, 152, 154, 157, 160, 179) or have obviously sinuous anticlinal walls [e.g. *Q. glabricupula* (Fig. 179), *Q. hondae* (Fig. 180), and *Q. gemelliflora* [(*Kochummen, K.M. 40670*] (Fig. 181)]. The stomata size in subgenus *Cyclobalanopsis* is 12.05–38.52 × 9.95–30.70 μm, with a length to width ratio 0.81 to 2.00. Extremely large stomata were occasionally detected in nine species. Some stomata located above the veins are much larger (usually of the cyclocytic type) than those in the intercostal area [e.g. in *Quercus chungii* (Fig. 86), *Q. albicaulis* (Fig. 163), *Quercus argentata* (Fig. 164), *Quercus tomentosinervis* (Fig. 165), and *Q. gemelliflora* (*Kochummen, K.M. 40670*) (Fig. 181)].

Stomatal wax chimneys were found in *Q. chungii* (Fig. 86) and *Quercus xanthotricha* (Fig. 87). Wax chimneys are barrel-like, composed of smaller and denser platelets in comparison to the epidermal wax platelet, and derive from a massive crust resulting from higher wax production of the epidermal cells surrounding the stomata.

Trichome types

Based on the number of cells in each one, trichomes can be classified as either simple or compound. Simple trichomes can be 'modules' of which compound trichomes are formed (Tschan & Denk, 2012). Individual cells of compound trichomes are sometimes difficult to distinguish in SEM but, using LM and considering the trichome base features, accurate identification of trichome types is feasible. Solitary, fasciculate, appressed laterally attached, simplified stellate, stellate, and stipitate, fasciculate trichomes are generally characterized by thick-walled cells. The constituent cells of uniseriate, branched uniseriate, and rosulate trichomes are usually thin-walled or intermediate between the thin-walled and thick-walled types. Nine trichome types were detected in subgenus *Cyclobalanopsis*, as described below.

Uniseriate (U) (Figs 37–40, 43, 47, 49, 51, 56, 61, 63, 67, 71, 74, 75, 78, 86, 88–102, 112, 114, 170, 172–180, 182, 187–193, 195)

Description: Thin-walled, multicellular trichomes usually with two to five cells arranged in one row. The diameter of the basal portion is 6.9–34.5 μm. Some uniseriate trichomes have large basal cells, which are distinct from other cells, appearing bulbous and much larger than the distal cells (Figs 170, 172–180, 187–193). In the typical uniseriate trichome, the basal and distal cells are similar in size. The trichome bases are small (Figs 182, 195) and easily distinguished from the trichome base of other thick-walled trichomes by their transparent to semi-transparent and less lignified cell walls. The trichome length is approximately 9.3–188.7 μm.

Occurrence: Uniseriate trichomes were found in all specimens investigated. They are easily broken, collapsed or sheared off, with only the basal portion remaining on the leaf epidermis. Uniseriate trichomes are better preserved in the intercostal regions than on the veins. In some species, two or three (to five) uniseriate trichomes are occasionally arranged in a row above the vein [e.g. *Q. austrocochinchinensis* (Fig. 187); *Q. mespilifolia* (Fig. 189); *Q. kerrii* (Fig. 190)].

Remarks: According to Jones (1986), this trichome type is the most basic glandular trichome and is generally present in Fagaceae. This trichome type is equivalent to the 'simple' trichome of Hardin (1976, 1979) who also recorded 'bulbous' trichomes, which he defined as the 'thin-walled, multicellular or enlarged portion, stipitate-glandular form'. However, these bulbous trichomes were a mixture of uniseriate (with distal cells swollen and uniseriate) and capitate (composed of a uniseriate stalk and a multicellular head) as defined by Jones (1986) and Tschan & Denk (2012).

Branched uniseriate (BU) (Figs 60, 103–105, 163–168)
Description: Thin-walled, multicellular trichomes, consisting of a unicellular stalk that is usually large. The trichome base is single-celled, diam. 12.8–21.5 µm, and transparent to semi-transparent as in uniseriate. On the top of the unicellular stalk, the distal cells branch into multiple long, thin membranous arms (Figs 60, 103–105, 166–168) and collapse very easily or break on dried specimens, with only the large basal portion or trichome base remaining (Figs 41, 42).

Occurrence: Found in eight species of subgenus *Cyclobalanopsis*, scattered on the lamina. The long membranous arms of different branched uniseriate trichomes sometimes join together to make a network structure (Figs 60, 103–105, 164–167).

Remarks: According to Jones (1986), branched uniseriate trichomes are irregular in shape, similar to the uniseriate trichome type, although they are branched at least once. The branched uniseriate trichomes observed in the present study exhibit elongate, fused membranous arms spreading radially, similar to the rosulate trichome but are distinguished by their large semi-transparent single-celled trichome bases (U-STB).

Rosulate (Ro) (Figs 146, 147, 191, 192, 195)
Description: Thin-walled and multicellular rosette trichomes, with a set of radiating, long, thin-walled, slender arms. The basal part of the arms may fuse together at the top of the basal cell. The trichome base is the typical compound trichome base, with a diameter of 20.1–34.8 µm. It forms a transparent, large membranous structure, with arms 190.0–245.8 µm.

Occurrence: Found only in *Q. sichourensis* (Figs 147, 192, 195) and *Quercus braianensis* (Figs 146, 191). This trichome type is persistent and forms a dense layer on the abaxial leaf surface, reflecting the light and giving a shiny appearance to the abaxial leaf surface.

Remarks: Luo & Zhou (2001) recorded the 'jellyfish trichome' in *Q. sichourensis*. This trichome is an extreme form of the rosulate trichome, since it is extremely thin (almost transparent), and large, with a diameter of 389.0–501.4 µm. The rosulate type is similar to the typical stellate trichome, except for its thin wall texture.

Simple solitary (S) (Fig. 162)
Description: Thick-walled, unicellular, acicular (needle-shaped). Its length varies on the same specimen. Simple solitary trichomes are usually smooth, straight and erect, not parallel to the leaf surface. The basal portion of the trichome attaches to the leaf epidermis directly. The trichome base is single-celled, the trichome base diameter is 9.6–17.9 µm and the basal portion is dark stained. The length of the trichome is 210.0–505.2 µm.

Occurrence: Found only in *Q. salicina* (*Deng*, *M. 4727*) in the present study, and mainly on or close to the veins, especially for the extremely long hairs.

Remarks: This trichome is the acicular trichome of Tschan & Denk (2012) and the solitary trichome of Hardin (1976, 1979). However, the acicular trichome of Tschan & Denk (2012) appears to be a mixture of solitary and appressed laterally attached trichomes. LM is necessary to identify the point of attachment of the trichome connected to the leaf epidermis in order to distinguish accurately solitary and appressed laterally attached trichomes from one another. Other similar trichome forms are also easily misidentified. For example, Luo & Zhou (2001: plate I-8) mistakenly classified the dark stained uniseriate to the solitary trichome in *Quercus glauca*, although the multicellular structure of the uniseriate can be readily detected under LM based on their plate. This underscores the importance of using both LM and SEM to investigate and classify plant trichomes.

Appressed laterally attached (ALA) (Figs 85, 106–116, 121, 128, 151–158)
Description: Thick-walled, similar to solitary, although the point of attachment to the epidermis of the appressed laterally attached trichome is at the side of the trichome instead of the base. As a result, it is more or less parallel to the epidermal surface, and does not

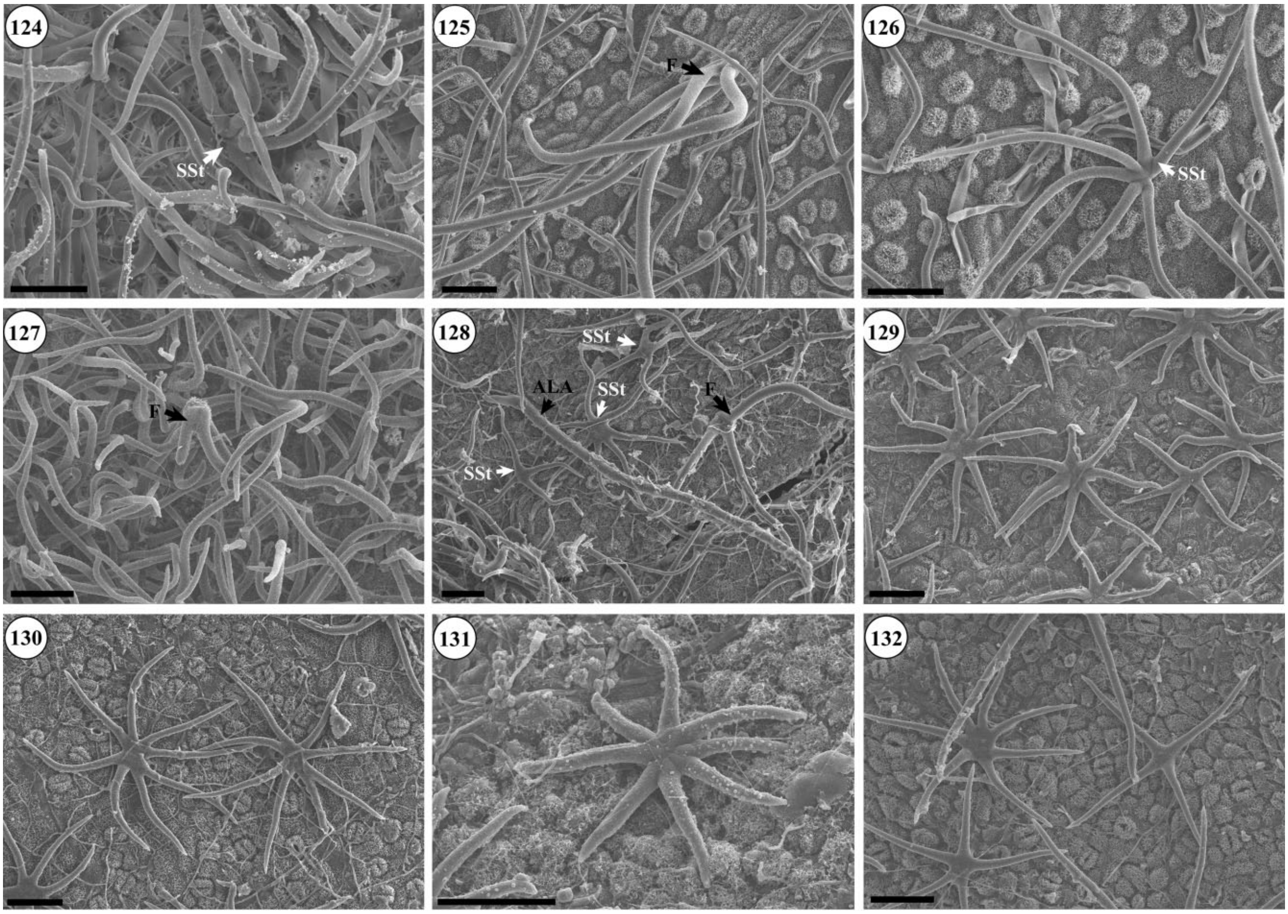

Figure 124–132. Scanning electron microscopy of leaf abaxial epidermis, showing SSt (124, 126, 128–132), fasciculate (F) (125, 127 & 128) and ALA (128); scale bar = 50 μm. 124. *Quercus gambleana*; 125, 126. *Quercus salicina* (Deng, M *et al.* 4727); 127. *Quercus argyrotricha*; 128. *Quercus ninganensis*; 129.*Quercus lowii*; 130. *Quercus percoriacea*; 131. *Quercus nivea*.; 132. *Quercus oidocarpa*.

have the erect form of the solitary trichome. The length of the appressed laterally attached trichome is 77.7–420.6 μm. The texture of the trichomes can be soft (e.g. *Quercus pseudoverticillata* (Fig. 85); *Quercus morii* (Fig. 112); *Quercus sumatrana* (Fig. 113)] to rigid [e.g. *Quercus xanthotricha* (Fig. 106); *Quercus thomsoniana* (Fig. 107); *Q. salicina* [*Deng, M. 3700*] (Fig. 109); *Quercus arbutifolia* (Fig. 121)]. The appressed laterally attached trichomes may be curly, with length in this case is 97.7–430.6 μm. In some species some tiny warts or spine-like protuberances can be found on the surface of appressed laterally attached trichomes, such as in *Quercus stewardiana* (Fig. 110) and *Q. arbutifolia* (Fig. 121). The trichome base of appressed laterally attached trichomes is single-celled and usually small. The whole basal portion is thick-walled and dark stained (STB) (Figs 152, 153, 160), which makes them easily distinguished from the single-celled trichome bases of thin-walled trichomes (U-STB).

Occurrence: Commonly present in subgenus *Cyclobalanopsis*, found on the veins and intercostal area, mostly with arms oriented parallel to the leaf surface.

Remarks: The appressed laterally attached trichome is the 'two-armed' trichome type of Metcalfe & Chalk (1950). It corresponds to the 'poils unicelluaires apprimes en navette' of Camus (1934–1954) and the 'appressed-lateral' of Hardin (1976). Some of the acicular hairs recorded by Tschan & Denk (2012) may be appressed laterally attached trichomes because they are parallel to the epidermal surface as shown by their figures (Tschan & Denk, 2012: figs 29, 35). Luo & Zhou (2001: plate II-7) reported the solitary trichome in several species of subgenus *Cyclobalanopsis*, although close inspection of their plates shows that the solitary trichomes they found were mistakenly identified appressed laterally attached trichomes.

Fasciculate (F) (Figs 125, 127, 128, 161, 162)
Description: Thick-walled, multicellular trichome. These are formed of clustered solitary or appressed laterally attached trichomes. This trichome type typically has two to eight arms, each 146.0–501.1 μm long. The trichome base is single-celled with a diameter of 7.1–18.2 μm. Extremely long, thick, fasciculate trichomes are found mainly on the veins or close to the vein area (Figs 125, 161, 162). The trichome base is without a pedestal structure.

Occurrence: Found in *Q. salicina*, *Quercus gambleana*, *Quercus argyrotricha*, *Quercus ninganensis*, and *Quercus brandisiana*, usually together with appressed laterally attached and solitary trichomes.

Notes: Extremely similar to stipitate fasciculate trichomes (SF) under SEM, although the trichome base is flat, single-celled or nontypical single-celled.

Simplified stellate (SSt) (Figs 117–120, 122–124, 126, 128, 129–132, 158–160, 182, 183)
Description: A cluster of appressed laterally attached or (and) solitary trichomes. It is multicellular, thick-walled, with a single set of (two) four to eight, radiating arms projecting horizontally from a common center. The length of each arm is 24.5–221.3 μm. The diameter of the trichome is 76.5–420.2 μm. Sometimes, simplified stellate and appressed laterally attached trichomes were both found on the same specimens (Figs 116–120, 121, 122, 128, 158). The trichome base is flat, without a pedestal structure, and is a nontypical single-celled trichome base (one side of the cell wall of the epidermal cell adjacent to the trichome base was thickened and dark-stained) [e.g. *Quercus percoriacea* (Fig. 158); *Q. disciformis* (Fig. 159); *Quercus oidocarpa* (Fig. 160), *Q. argyrotricha* (Fig. 182), and *Q. lowii* (Fig. 183)].

Occurrence: Found in 13 specimens (representing 11 species) of subgenus *Cyclobalanopsis* scattered on the abaxial surface of the leaves and usually occurring with appressed laterally attached or solitary trichomes.

Remarks: As seen under SEM, the morphology of the simplified stellate trichome is close to that of the typical stellate trichome, although the latter has a prominent compound trichome base (pedestal) above the epidermis, which was darkly stained under LM and may be related to a secretory function. ‘Bifurcate’ trichomes recorded by Tschan & Denk (2012) are bicellular, double or twin trichomes, consisting of two arms originating from a common point. In the present study, we found the same trichome type with two to six arms on one specimen, together with appressed laterally attached trichomes [e.g. in *Quercus subsericea* (Figs 126–130), *Q. arbutifolia* (Figs 116–120), and *Q. percoriacea* (Fig. 158)]. In specimens with both ALA and SSt, the appearance of the arms of the two trichome types was similar. Both of their arms had an irregular convex decoration and a long arm axis parallel to the leaf surface but with more arms in SSt.

Stellate (St) (Figs 139–145, 184–186)
Description: Multicellular, thick-walled, with (seven) eight to 34 arms radiating from a common origin and parallel to the epidermis or radiating in different directions. The diameter of the trichome is 110.2–389.0 μm. The arm length is 47.82–194.00 μm. There is some variation in the basal part of the arms. The arms can be fused only at the base and diverge from one point, or fused for a significant portion of their length. The trichome base is the compound type, diameter 18.3–37.7 μm. When stellate trichomes fell from the leaf surface, crystals were detected in the compound trichome base (Fig. 150). Generally, stellate trichomes were persistent and formed a dense yellow indumentum.

Occurrence: Detected in nine specimens (representing seven species). They are found predominantly in the intercostal regions of the abaxial leaf surface. Although we did not find stellate trichomes on the adaxial leaf epidermis, we did detect compound trichome bases, indicating their existence at an early stage of leaf development.

Remarks: The appearance of simplified stellate and stellate trichomes is similar. The key differences between the two kinds of trichome are mainly in their bases. There is no pedestal structure in the base of simplified stellate trichomes but, in stellate trichomes, the compound trichome base forms a pedestal-like structure. The pedestal portion can be easily detected by LM, rather than SEM. Hardin (1976, 1979) and Jones (1986) also reported fused stellate and multiradiate trichomes. However, we found it difficult to identify those subtypes accurately because the basal portion of the arms more or less fused together into a discoid or globular form. The percentage of the fusion of the arms varies, even on the same specimen. Therefore, we agree with Tschan & Denk (2012) and regard the fused stellate and multiradiate trichomes as variations of the stellate trichome.

Stipitate fasciculate (SF) (Figs 133–138)
Description: Multicellular, thick-walled, usually with six to nine arms, arm length 146.0–484.5 μm. All the arms radiate but are not parallel to the epidermis; there is a prominent compound trichome base (pedestal structure) (Figs 148–150), diameter 26.2–

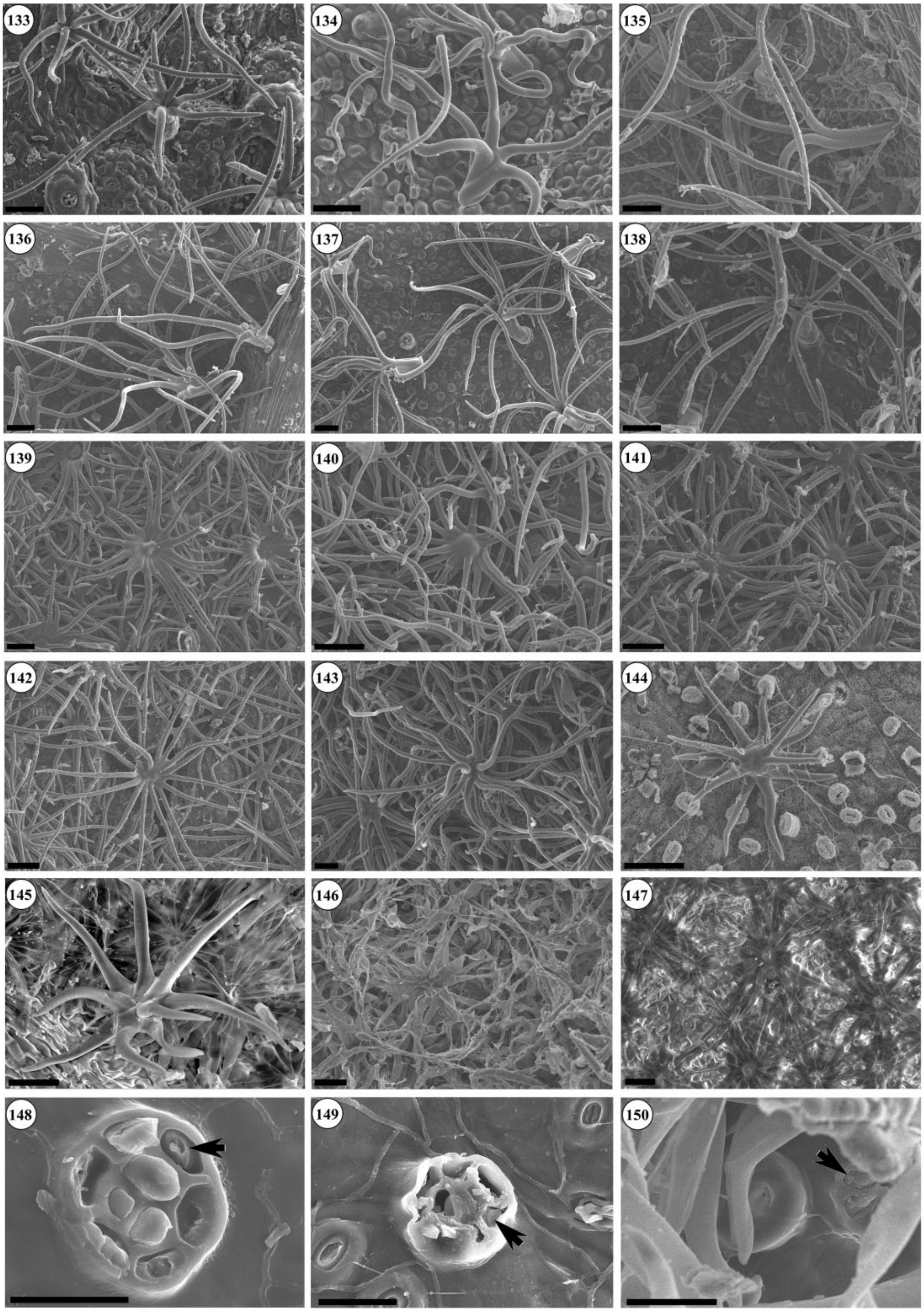

Figure 133–150. Scanning electron microscopy of leaf abaxial epidermis, showing trichomes with compound trichome base; scale bar = 50 µm. 133–138. Fasiculate trichomes. 133. *Quercus helferiana*; 134. *Quercus rex*; 135. *Quercus brandisiana*; 136. *Quercus austrocochinchinensis*; 137. *Quercus thorelii*; 138. *Quercus kerrii*; 139–145. Stellate trichomes. 139. *Quercus championii*; 140. *Quercus mespilifolia* (Alan, 10284); 141. *Quercus lobbii* (Mause, G. 445-8); 142. *Quercus delavayi*; 143. *Quercus gilva*; 144. *Quercus chungii*; 145. *Quercus sichourensis*; 146–147. Rosulate trichomes. 146. *Quercus braianensis*; 147. *Quercus sichourensis*; 148–150. CTB with crystals inside locule (shown by arrows). 148. *Quercus austrocochinchiensis*; 149. *Quercus helferiana*; 150. *Quercus mespilifolia* (Alan, 10284).

49.7 μm, which is slightly above the epidermal cells and dark stained by LM (Figs 187–190, 193). Crystal structures were also detected in collenchyma cells composing the compound trichome base (Figs 148, 149). The arms are fused for a considerable length at the basal portion (Figs 133–138) as described by Jones (1986).

Occurrence: Found in seven specimens (representing six species). They were prominent at the juvenile stage on the leaf but are easily lost as the leaf matures. They were commonly found on the abaxial surface and were generally better preserved close to the primary and secondary vein areas.

Remarks: Sometimes, it is difficult to distinguish fasciculate from stipitate fasciculate trichomes. The prominent compound trichome base (which forms a pedestal structure) of stipitate, fasciculate trichomes offers an ideal feature to separate them from fasciculate trichomes because, in the latter, the trichome base is flat and single-celled.

Trichome base (Figs 148–180, 182–195)

Trichomes are generally present on leaves in oaks, especially at their juvenile stage. Some of the trichomes are lost as the leaves mature, with only trichome bases remaining on the leaf epidermis (see Supporting information, Table S1). The morphology of trichome bases was more easily detected by LM than SEM. Two main trichome base types were found in subgenus *Cyclobalanopsis*.

Single-celled trichome bases

Description: The cell wall of the trichome base was usually cutinized and stained more darkly than the epidermal cells. There were two main subtypes of the single-celled trichome base, which can be classified easily according to the texture of the trichome. (1) The single-celled trichome base of the thin-walled trichomes (including uniseriate and branched uniseriate) (U-STB) is larger than other cells of the trichome (diameter 6.5–33.4 μm), and transparent to semi-transparent (Figs 151–153, 155, 156, 158, 160, 161, 163–170, 172–180, 182, 185, 187–193, 195); (2) The single-celled trichome base of thick-walled trichomes (including ALA, S, F and SSt) (STB) is flat, highly cutinized, and darkly stained. Its is smaller than U-STB, diameter 4.5–18.4 [e.g. trichome bases of ALA (Figs 151–158), SSt (Figs 158, 159, 160, 182, 183), F and S (Fig. 162)]. The epidermal cells around the trichome base can be unmodified (Figs 151–158) or they may be smaller than other epidermal cells (Figs 169, 171, 172, 178). In some extreme cases, such as simplified stellate and fasciculate trichomes (Figs 182, 183), the epidermal cell wall adjacent to the side of the trichome base is cutinized, although it remains flat, without a pedestal structure.

Compound trichome bases (CTB) (Figs 148–150, 184–195)

Descriptions: These formed a pedestal structure above the other leaf epidermal cells. They are usually composed of (four-) five to eight darkly stained cells, which gives the appearance of a 'flower-like' structure by LM (Figs 184–195). When the stipitate fasciculate, stellate, and rosulate trichomes were broken off, crystals are found in the locules of the trichome base cells (Figs 148–150), which indicates that the compound trichome base may perform a secretory function. This structure makes it easy to distinguish stipitate fasciculate, stellate, and rosulate trichomes from similar trichome forms with single-celled trichome bases.

Mapping of the characters onto the ITS cladogram and cladistic analysis of leaf epidermal features

We mapped 16 important and stable leaf epidermal features onto the ITS consensus tree of Deng *et al*. (2013b) (Fig. 196A). Our results demonstrate that many of the epidermal features are homoplastic (i.e. derived and/or lost more than once). The compound trichome base was a synapomorphy of the clade section *Cerris* + CTB group. Some features were autapomorphies (e.g. the solitary and fasciculate trichomes of *Q. salicina*, the capitate trichome of *Q. acrodonta*, and the rosulate trichome of *Q. sichourensis*. U-STB and STB represent the plesiomorphic state) (Fig. 196A).

The cladistic analysis of the 17 leaf epidermal features revealed two main clades in *Quercus* subgenus *Cyclobalanopsis* and *Quercus* section *Cerris* (Fig. 196C). One clade was composed of the species with a compound trichome base from *Quercus* section *Cerris* and subgenus *Cyclobalanopsis* (bootstrap = 63%); however, both subgenus *Cyclobalanopsis* and section *Cerris* are paraphyletic in this clade. The other species without CTB formed another clade (STB clade), except for *Quercus edithae*, which does not have sufficient characters to place it in either clade. A few subclades characterized by different distinct trichome types can be detected in the STB clade (e.g. the BU subclade was composed of the two species with branched uniseriate trichomes, whereas the ALA subclade was composed of species with ALA trichomes).

DISCUSSION

Comparison of trichome types in *Quercus s.l.* from previous studies and refinement of trichome terminology

As an important Northern Hemisphere genus, *Quercus* has been well characterized in previous

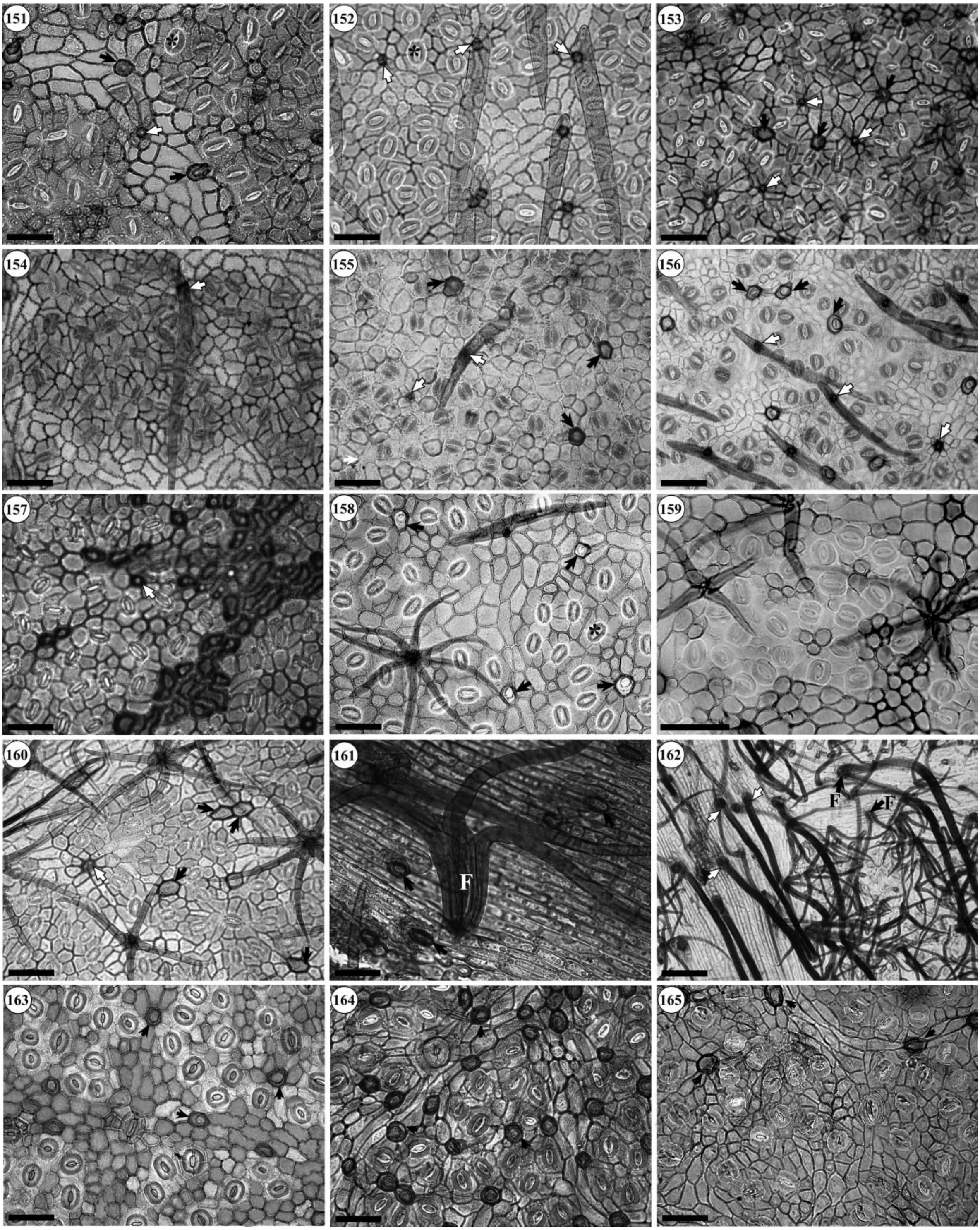

Figure 151–165. Leaf abaxial epidermis under light microscopy (× 40 objective lens), showing the U or BU with U-STB (shown by black arrow), ALA, F and SSt with STB (show by white arrow); *nontypical cyclocytic stomata; scale bar = 50 μm. 151. *Quercus glauca* (ALA, U); 152. *Quercus annulata* (ALA); 153. *Quercus tranninhensis* (ALA, U); 154. *Quercus stenophylloides* (ALA); 155. *Quercus sumatrana* (ALA, U); 156. *Quercus thomsoniana* (ALA, U); 157. *Quercus subsericea* (ALA); 158. *Quercus percoriacea* (ALA, SSt, U); 159. *Quercus disciformis* (SSt); 160. *Quercus oidocarpa* (SSt, U); 161. *Quercus brandisiana* (F, U); 162. *Quercus salicina* (Deng, M *et al*. 4727) (S, F); 163. *Quercus albicaulis* (BU); 164. *Quercus argentata* (BU); 165. *Quercus tomentosinervis* (BU).

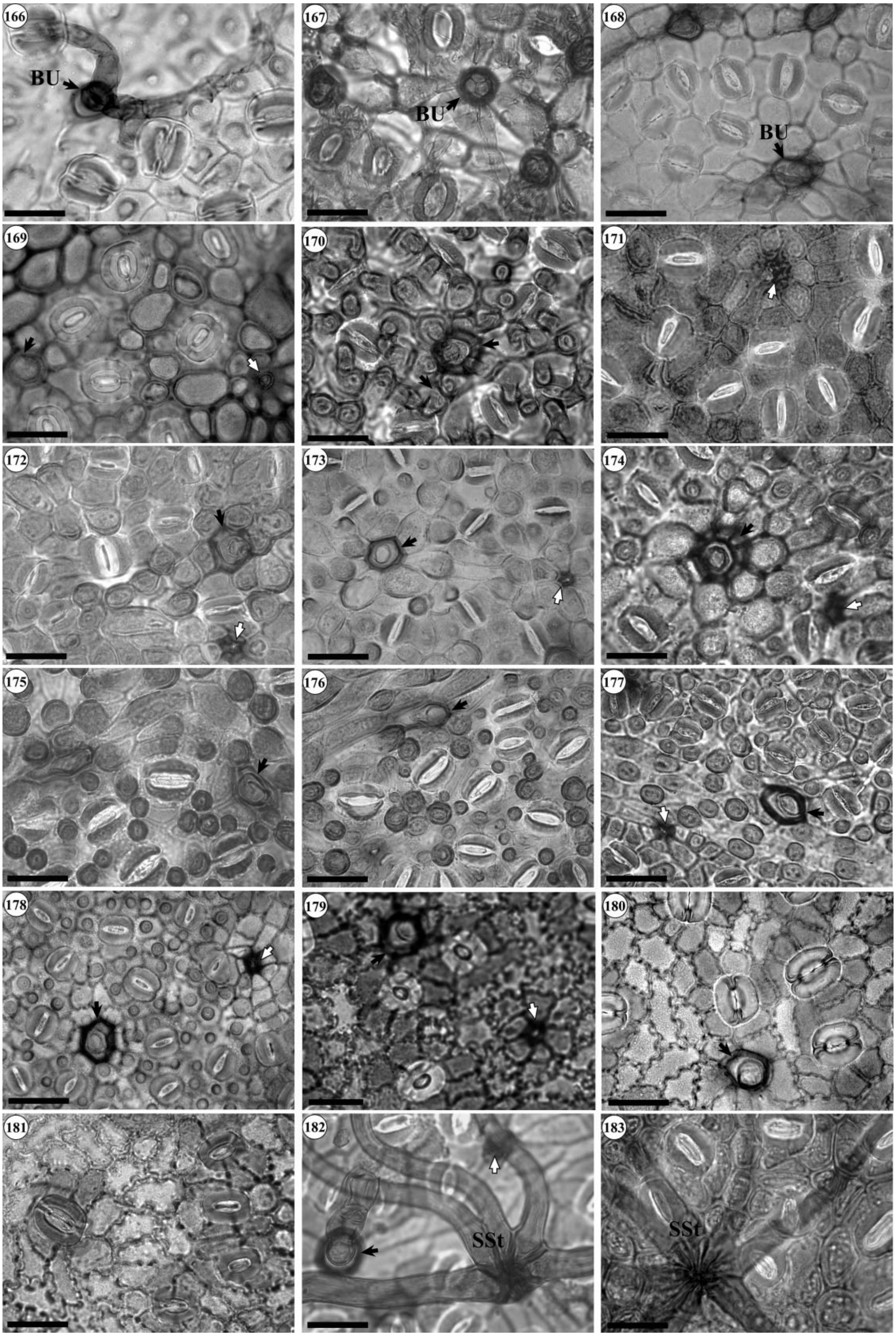

Figure 166–183. See caption on next page.

Figure 166–183. Leaf abaxial epidermis under light microscopy (× 100 objective lens), showing the single-celled trichome base types of different trichome types, white arrow indicating STB, black arrow indicating U-STB, stomata types (An: anomocytic stomata; Cyc: cyclocytic stomata) and epidermal cell shapes (Pa: papillae thickening; sin: sinuous anticlinal wall); scale bar = 20 μm. 166. *Quercus jenseniana* (BU, Pa, An); 167. *Quercus argentata* (BU, An); 168. *Quercus augustinii* (BU, An); 169. *Quercus rupestris* (Cyc); 170. *Quercus elmeri* (Pa, An/Cyc); 171. *Quercus brevicalyx* (Kerr, A.F.G. 21017); 172. *Quercus treubiana* (Kostermans, S.A. 7442, Cyc); 173. *Quercus kouangsiensis* (Pa, U-STB, STB, Cyc); 174. *Quercus gemelliflora* (Medan, 45417) (Pa, An); 175. *Quercus gaharuensis* (Pap, An); 176. *Quercus valdinervosa* (Pap, An); 177. *Quercus ramsbottomii* (Pa, An); 178. *Quercus semiserrata* (Pa, An); 179. *Quercus glabricupula* (U-STB, sin, Cyc); 180. *Quercus hondae* (U-STB, sin, Cyc); 181. *Quercus gemelliflora* (Kochummen, K.M. 40670) (sin, Cyc); 182. *Quercus argyrotricha* (U, U-STB, STB, SSt); 183. *Quercus lowii* (SSt, STB).

studies in terms of its diverse leaf trichome types and leaf epidermal features (Hardin, 1975, 1976, 1979; Jones, 1986; Bussotti & Grossoni, 1997; Luo & Zhou, 2001; Tschan & Denk, 2012). However, inconsistent trichome terminology and nomenclature in previous studies have caused considerable confusion in trichome classification (Table 1). Jones (1986) enumerated nine trichome types in subgenus *Cyclobalanopsis*, (solitary, appressed laterally attached, fasciculate, stellate, fused stellate, stipitate fasciculate, rosulate, simple uniseriate, and papillae, although papillae are a thickening ornamentation on epidermal cells rather than a trichome type); and three other trichome types, found only in subgenus *Quercus*: multiradiate, capitate, and branched uniseriate. The trichome terminology applied by Hardin (1975, 1976, 1979) was similar to that of Jones (1986), with differences in simple-branched and bulbous trichomes, which were equivalent to the branched uniseriate and capitate trichomes, respectively, of Jones (1986). Tschan & Denk (2012) regarded fused stellate and multiradiate trichomes as the same type as stellate trichomes. This classification partly agrees with the present study because it is difficult to separate these similar types. However, their work did not record the trichome base features of the stellate-like trichomes. As a result, it is difficult to catalogue the stellate trichome and simplified stellate trichome types from their studies.

Burrows *et al*. (2013) used fluorescent tracer dyes to explore the functions of the trichomes and trichome base in *Solanum elaeagnifolium* Cav. Their results illustrated the downward projections of intrusive basal cells of the stellate trichomes of this species clearly, although small chloroplasts were detected in both the stellate trichomes and their intrusive stalk base, which indicated they remained alive for most of the life of a leaf. Their results did not support a transport function for the trichomes but suggested that their function was probably to protect the mesophyll cells from invertebrate herbivory and decrease radiation absorption. In the present study, we found the presence of crystals in the locule of the compound trichome base, which suggests that this structure and related trichome types may perform secretory functions (e.g. for defence against insects) while the trichomes with only a single-celled base may have different functions. However, the relationship between trichomes and transport into and out of leaves is highly complex and needs to be assessed on an individual species basis (Burrows *et al*., 2013). As a result, the trichomes with a similar appearance, such as the simple stellate trichome (with STB) versus the stellate trichome (with CTB), fasciculate (with STB) versus stipitate fasciculate (with CTB), should be treated as different trichome types because they might have different ecological functions.

In the present study, we also found appressed laterally attached and simplified stellate trichomes (with two to six arms) on the same specimens (Figs 116–122, 158). The morphology of the two trichome types is highly similar, except for the number of arms. Tschan & Denk (2012) used 'modular' to indicate that the unicelluar trichome can form other complex trichome types. The coexistence of ALA and two- to six-armed SSt and the strong similarity between the two trichome types in the present study suggests that SSt might be the derived form of ALA. The 'bifurcate' trichome described by Tschan & Denk (2012) represents the extreme stage of the simplified stellate trichome and should be attributed to the same trichome type as well. The 'acicular' trichome types that Tschan & Denk (2012) describe as 'unicellular, single hair, acicular; hairs often undulated, occasionally twisted, protruding, rarely appressed to epidermis' are equivalent to 'solitary' as described by Jones (1986). The acicular (solitary) trichome is attached to the epidermis at the base but, in the appressed laterally attached trichome, the point of attachment is vertical to the long axis of the trichome and the point of attachment divides the trichome into arms of equal or unequal length, with each end of the arms free from the epidermis. The morphological diversity of appressed laterally attached trichomes was well illustrated by Camus (1934–1954: atlas I, pls.III, IV, VI, VII, X, XI, XIV). However, these two trichome types can be easily confused without LM to assist in identifying the attachment point of the

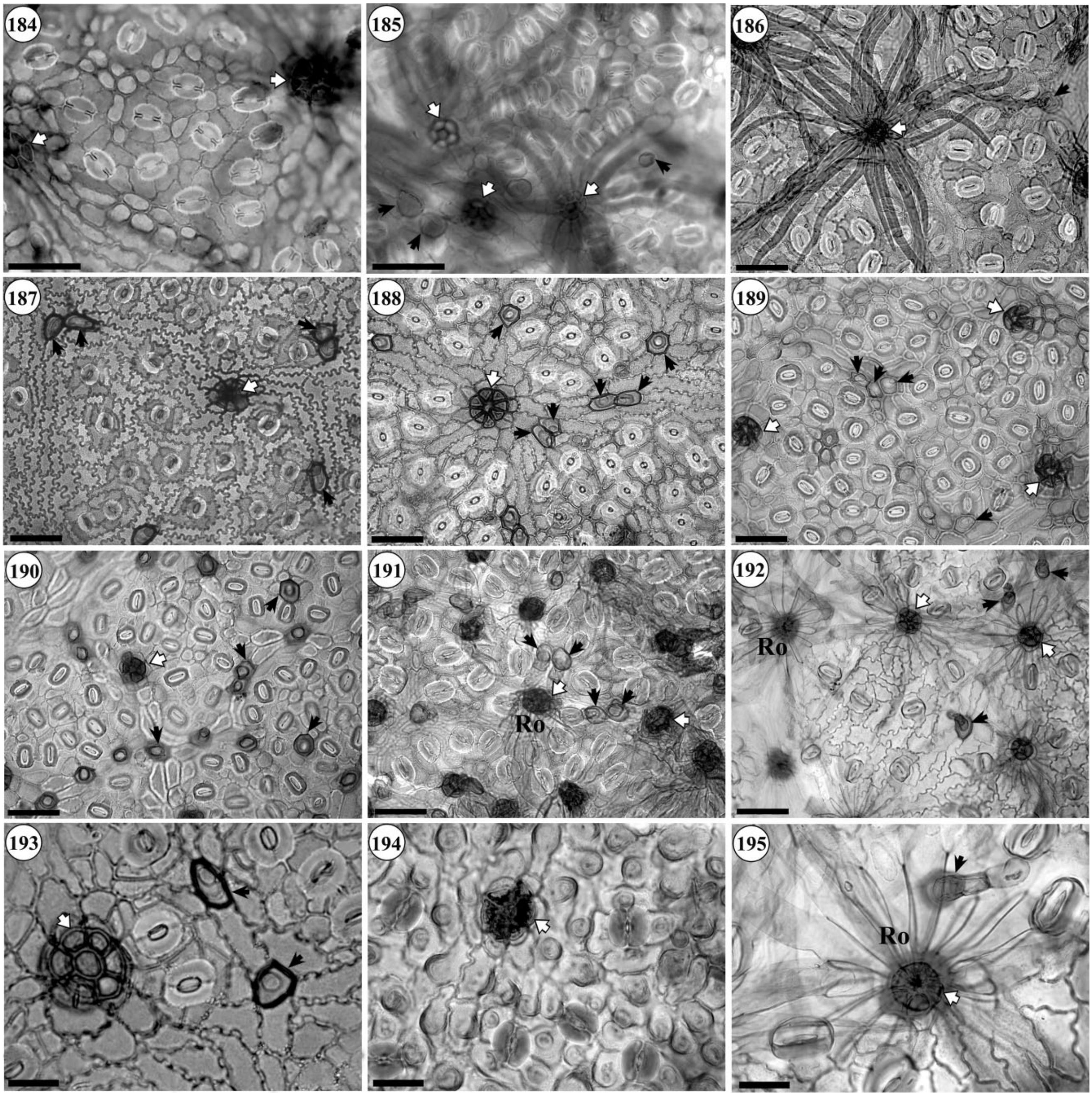

Figure 184–195. Leaf abaxial epidermis under light microscopy (× 40 objective lens) (I). Showing trichomes with compound trichome base (CTB) and stomata and epidermal cell features; white arrow indicating CTB; black arrow indicating U-STB; 184–192, scale bar = 50 μm; 193–195, scale bar = 20 μm. 184. *Quercus gilva* (St, CTB, Cyc); 185. *Quercus delavayi* (St, CTB, Cyc); 186. *Quercus lobbii* (Clarke, C.B. 15451; St, CTB, An); 187. *Quercus austrocochinchinensis* (U, CTB, Cyc); 188. *Quercus gomeziana* (Brandis, D. 530; U, CTB, An); 189. *Quercus mespilifolia* (Alan, 10284; U, CTB, An; 190. *Quercus kerrii* (U, CTB, An); 191. *Quercus braianensis* (Ro, U, CTB, An); 192 & 195. *Quercus sichourensis* (Ro, U, CTB, An); 193. *Quercus thorelii* (U, CTB, Cyc); 194. *Quercus rex* (Pap, CTB, An).

trichome to the epidermis (Figs 152, 155, 156). Therefore, some 'acicular' trichomes of Tschan & Denk (2012: figs 29, 30) are suspected to be appressed laterally attached trichomes. The solitary trichomes reported by Luo & Zhou (2001) are also a mixture of the solitary, uniseriate (Luo & Zhou, 2001: plate I-8) and appressed laterally attached trichomes (Luo & Zhou, 2001: plate II-7). Adding the trichome base characters to the profile of trichome morphology can greatly improve the accuracy of identifying trichome

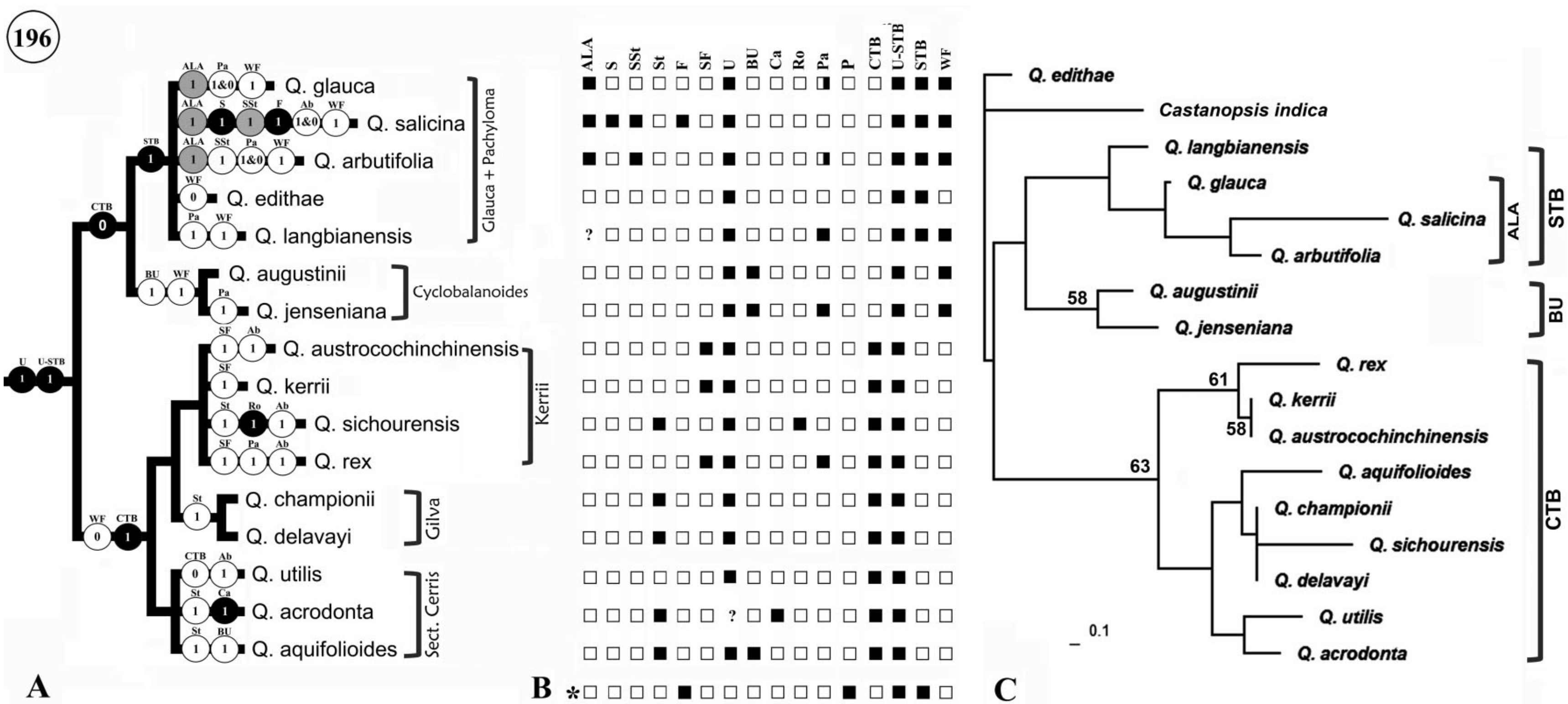

Figure 196. Distribution of leaf epidermal features in subgenus *Cyclobalanopsis* and selected evergreen species in section Cerris based on a simplified maximum parsimony tree of internal transcribed spacer sequence data obtained by Deng *et al*. (2013b) and cladistic analysis of 17 leaf epidermal features. A, leaf epidermal evolutionary pattern. Black solid circles indicate the plesiomorphism/synapomorphism/autapomorphism. A grey solid circle indicates that the evolutionary pattern is unknown as a result of poor resolution at these nodes. An empty circle indicates the paraphyletic status of those features. B, the states of scored leaf epidermal features. White square: 0; black square: 1; *marked line represents the coded leaf epidermal features of *Castanopsis indica*; C, Neigbor joining tree based on 17 leaf epidermal features using PAUP 4.01b. Bootstrap values (%) were indicated above the branches (consistency index = 0.519; retention idex = 0.589). WF, wax flake.

types and reduce the homoplasy when tracing the evolutionary patterns of those epidermal features. However, the trichome base can only be detected by LM, and observing the leaf epidermal features by LM and SEM is thus essential for defining the trichome type. Currently, most of the studies on trichome type are mainly based on SEM, which makes a lot of trichomes with a similar appearance hard to define (e.g. fasiciculate versus stipitate fasciculate; stellate versus simplified stellate; solitary versus appressed laterally attached). The trichome types in oaks still need further complementary study.

Diversity of leaf epidermal features in subgenus *Cyclobalanopsis*

Based on leaf epidermal features, three main groups of species were found in the present study.

1. Compound trichome base group (CTB group). The species in this group all have a prominent compound trichome base (with pedestal structure) and a smooth wax layer on the leaf abaxial epidermis, except for *Q. chungii*. This group was also supported by cladistic analysis of leaf traits (Fig. 196C) and optimization of traits onto the ITS topology (Fig. 196A).
2. Branched uniseriate group (BU group). The species in this group have branched uniseriate trichomes on their abaxial leaf epidermis (Figs 103–105, 163–168). Their cupules have concentric lamellae, which are mostly fused to the cupule wall, with only the rims free. Barnett (1944) and Menitsky (1984) treated these species as the group *Oidocarpa* Korth. and section *Cyclobalanoides*, respectively. Both leaf anatomy and cupule features indicate that the BU group forms a natural clade in subgenus *Cyclobalanopsis*.
3. Single-celled trichome base group (STB group). This is the most diverse group in subgenus *Cyclobalanopsis*. Its distribution covers almost the whole the geographic range of the subgenus. Except for the most commonly present uniseriate trichome (with U-STB), the typical STB of thick-walled trichomes were generally found on the leaf epidermis of this group. Appressed laterally attached trichomes are generally present in this group. Other trichome types such as the solitary, simplified stellate, and fasciculate trichomes are also found. In the present study, we did not find trichomes in some species (see Supporting information, Table S1), although the presence of STB trichome bases (the corresponding trichome: ALA, S, F, SSt) and U-STB (the corresponding trichomes U and BU) suggested the presence of these trichomes at the juvenile leaf stage. Further epidermal studies at different stages of leaf development are needed to clarify these missing trichome types and their dynamic changes during different growth stages.

Taxonomic implications of leaf epidermal features for the taxonomy of subgenus *Cyclobalanopsis* and variation of leaf epidermal features within a species

In the present study, two or three specimens of each of 15 species were studied. In most cases, the leaf trichome types are considered to be less affected by environment and certain trichomes are restricted to particular subgenera/series in oaks (Hardin, 1979). Other leaf features, for example, epidermal cell and stomatal morphology were similar within species in subgenus *Cyclobalanopsis* (Deng, 2007). These leaf epidermal features have obvious taxonomic implications [e.g. the epidermal features of the species pairs *Q. glauca* and *Quercus tranninhensis*, *Quercus asymmetrica* and *Quercus patelliformis*, and *Quercus brevicalyx* and *Quercus yingjiangensis* were almost identical, supporting the recognition of *Q. tranninhensis* as a synonym of *Q. glauca*) (Govaerts & Frodin, 1998), *Q. patelliformis* as a synonym of *Q. asymmetrica*, and *Q. yingjiangensis* as a synonym of *Q. brevicalyx* by Deng, Zhou & Coombes (2010). However, in the two specimens identified as *Q. gemelliflora*, papilla thickening on epidermal cells, and straight to curved anticlinal cell walls were found on the specimen *Medan 45417* (Figs 174), although flat epidermal cells with prominent sinuous anticlinal cell walls were found in the specimen *Kochummen*, *K.M. 40670* (Fig. 181). These significant differences in leaf epidermal features indicate that the two specimens might represent two different taxa. *Quercus glabricupula* was accepted as a synonym of *Q. augustinii* by Govaerts & Frodin (1998), although the difference of leaf epidermal features of *Q. glabricupula* and *Q. augustinii* were significant [e.g. anomocytic stomata, straight to curved anticlinal walls on the abaxial leaf epidermal cells and semi-transparent trichome bases in *Q. augustinii* (Fig. 166) versus cyclocytic stomata, sinuous anticlinal cell walls and a small cutinized trichome base in *Q. glabricupula* (Fig. 179)]. Similarly, *Quercus wangsaiensis* and *Quercus longistyla* were listed as synonyms of *Quercus quangtriensis* by Phengklai (2006). Papilla thickening on epidermal cells was found in *Q. quangtriensis* but not in *Q. longistyla* and *Q. wangsaiensis*, suggesting the taxonomic status of these three species deserves further investigation. Further comprehensive studies of more herbarium material of the same taxa and field observations of leaf trichome variation at different stages of leaf development are essential for exploring the true identities of these species. As noted above, the leaf epidermal features, especially the trichome type, trichome base type, anticlinal cell wall and the thickening on leaf abaxial epidermal cells were mostly stable in oak species (Hardin, 1979; Deng, 2007). These features are valuable for identification of species in subgenus *Cyclobalanopsis*, and offer tools to identify herbarium specimens.

Diversity of leaf epidermal morphology of oaks in the Old-World clade (section *Cerris* + subgenus *Cyclobalanopsis*)

The nine trichome types, two wax flake types, two stomatal aperture types, and single-celled and compound trichome base types detected in subgenus *Cyclobalanopsis* were also found in subgenus *Quercus*, which supports the inclusion of *Cyclobalanopsis* in *Quercus*.

Currently, ITS-based phylogenetic studies can only suggest that there are two main clades (four subgroups) of subgenus *Cyclobalanopsis*: [section *Cerris* + (*Kerrii* group + *Delavayi* group)] + [(*Glauca* group + *Pachyloma* group)] (Fig. 196A), although without robust bootstrap support (Deng *et al*., 2013b). This topology was partly supported by the cladistic analysis of leaf epidermal characters. Although most leaf epidermal features were homoplastic on the ITS cladogram, many nonetheless exhibit strong phylogenetic signals. The compound trichome base present in the CTB group of subgenus *Cylcoblanaopsis* and section *Cerris* is a synapomorphy supporting the ITS topology. While parsimony optimization of character states on a tree is not ideally suited to reconstructing the history of trait evolution, it appears based on our analysis that section *Cerris* and the CTB group of subgenus *Cyclobalanopsis* originated from an ancestor with a smooth wax layer and a compound trichome base. Our results also suggest that the rest of the STB group of species of subgenus *Cyclobalanopsis* were derived from an ancestor with a single-celled trichome base and platelet wax flakes, but that some species of the STB group acquired the smooth wax layer later. Branched uniseriate trichomes have been found in several species in section *Cerris* (Camus, 1934–1954; Zhou *et al*., 1995; Yang *et al*., 2012) and in the BU group of subgenus *Cyclobalanopsis* in the present study. This trichome type was apparently derived independently and paraphyletically in different clades of the Old-World oak clade (Fig. 196), but the trait still serves as a synapomorphy for the 'Cyclobalanoides' group (BU group). A large number of leaf epidermal features show a paraphyletic pattern, although they are still informative for the taxonomy of these oaks.

The presence of the various trichome types is also related to the developmental stage of the leaves. The single-celled trichome base was found in all the species. Although, in some species, no trichomes were detected on both leaf surfaces by SEM, the existence of single-celled trichome bases on the leaf epidermis demonstrates the existence of related trichome types in juvenile leaves. Further studies to compare the trichome type variations at different growth stages, and in different geographical populations, are needed to illustrate the morphological variations of trichomes in subgenus *Cyclobalanopsis* better.

Bussotti & Grossoni (1997) and Zhou *et al*. (1995) found the smooth wax flake layer in section *Cerris*, and the vertical scales (platelet) wax flakes in section *Quercus.* The morphology of epicuticular wax provided useful characteristics to group the species in subgenus *Quercus*. Both epicuticular wax types were found in subgenus *Cyclcobalanopsis*, although this feature also showed a paraphyletic pattern in this subgenus. Most of the species with a compound trichome base have smooth wax layers (except for *Q. chungii*). This is partly supported by the ITS-based phylogenetic tree for *Quercus s.l and* suggests that the CTB group of species of subgenus *Cyclobalanopsis* might be the first-branching clade and has a closer relationship to section *Cerris* (Deng *et al*., 2013b). However, the smooth wax layer is also found in other species without a compound trichome base from tropical, low mountain areas (e.g. *Quercus phanera*, *Q. disciformis*, and *Q. rupestris*). The platelet wax ornamentation is mainly found in species from subtropical or tropical, high mountain areas. Therefore, the wax flake feature not only has a genetic basis, but also is related to climatic factors. Further studies on epicuticular wax morphology of different populations are needed to reveal its ecological functions.

The significance of leaf epidermal characters for intra- and intergeneric relationships in *Quercus* and Fagaceae

The trichome types of subgenus *Cyclobalanopsis* were consistent with those of subgenus *Quercus*, and most of the trichome types were shared with other genera of Fagaceae, although some differences in leaf epidermal features were found in the present study. The papillae on leaf epidermal cells were found in subgenus *Cyclobalanopsis* but not in subgenus *Quercus*. The papillae were also found in some species of *Lithocarpus* Blume. However, those *Lithocarpus* spp. all had appressed parallel tuft trichomes (APT) (in which the trichome bases are swollen, not dark stained, and are arranged in a circle surrounding the stomata), as well as peltate trichomes (which had free rims and a thin-walled trichome) (Deng *et al*., 2013a).

These distinct characteristics make the leaves of *Lithocarpus* easily distinguished from those of *Quercus* subgenus *Cyclobalanopsis* by LM.

The compound trichome base of *Quercus s.l.* differs from those in other genera of Fagaceae in the dark stained trichome base that forms a pedestal structure. Although fasciculate trichomes were also found in some species of *Castanopsis* and *Lithocarpus*, the trichome base in those species did not have a pedestal structure.

The stomata type was typical cyclocytic in *Lithocarpus* and *Castanopsis* because the subsidiary cells were usually much smaller than the other epidermal cells. They typically form a ring around the stomata (Liu *et al*., 2009; Deng *et al*., 2013a). The shared subsidiary cells between stomata were rarely shared in *Castanopsis* (Liu *et al*., 2009) and *Lithocarpus* (Deng *et al*., 2013a). Most of the cyclocytic stomata in *Quercus* subgenus *Cyclobalanopsis* were not typical because the size of the subsidiary cells was similar to that of other leaf epidermal cells (Fig. 179–181). These subsidiary cells were commonly shared among the stomata. The comparison of the stomatal and epidermal features documented by Zhou *et al*. (1995) from subgenus *Quercus* of China shows the aperture rims of stomata can be slightly projecting, flat or occasionally slightly sunken in species of *Quercus* section *Cerris* but not in subgenus *Cyclobalanopsis*. The subsidiary cell size, aperture rims and subsidiary cell arrangement can be seen as informative diagnostic features to distinguish *Quercus* subgenus *Cyclobalanopsis* from *Quercus* section *Cerris*.

As a fossil-rich group, solid leaf fossil records of *Quercus s.l.* dating from the Tertiary have been reported from multiple sites in the Northern Hemisphere (Guo, 1978, 2011; Daghlian & Crepet, 1983; Uzunova *et al*., 1997; Xiao *et al*., 2006; Kvacek, 2010). The venation is generally preserved in the leaf fossils and is able to reveal their identities at the generic, sectional and even at species level. However, in Fagaceae, leaf architecture shows some degree of homoplasy, especially in subtropical evergreen genera, such as *Lithocarpus*, *Castanopsis*, and *Quercus* subgenus *Cyclobalanopsis* (Jones, 1986). In most cases, the trichomes are not preserved in fossil leaves, except for their bases. In such cases, the stomata and trichome bases of the leaf epidermis are extremely useful in determining the identity of fossil taxa. Combining leaf epidermal features and venation patterns of fossil taxa, it is possible to find their most closely-related extant species. For example, prominent compound trichome bases, typical cyclocytic stomata, and distally toothed leaf margins with intersecondary veins were found in Miocene fossil leaves of *Quercus praedelavayi* Y.W.Xing and Z.K.Zhou, (Xing *et al*., 2013) and *Quercus tenuipilosa* Q.Hu & Z.K.Zhou (Hu *et al*., 2014). All these features demonstrated that these two fossil taxa are most closely related to the extant *Q. delavayi* (subgenus *Cyclobalanopsis*). Therefore, the leaf trichome base has great taxonomic value in oak taxonomy. However, this character can only be detected by LM. In the future, well documented leaf epidermal studies using both LM and SEM could improve the accuracy of fossil identification and identify the most closely-related extant species. Such studies offer great opportunities to use these leaf fossils as calibrations to estimate precise divergence times of different clades based on molecular phylogenetic analyses of *Quercus s.l.*

Conclusions

In the present study, we comprehensively surveyed the leaf epidermal features of *Quercus* subgenus *Cyclobalanopsis* and refined trichome terminology in *Quercus s.l.* Nine trichome types (including three thin-walled and six thick-walled) were detected and defined. Two main trichome base types STB (including subtypes U-STB and STB) and CTB were found. Both LM and SEM are essential for accurately identifying trichome types in oaks. The leaf epidermal features in subgenus *Cyclobalanopsis* show considerable variation and reveal three main groups (CTB group, STB group, and BU group). This grouping was also supported by cladistic analysis of leaf epidermal features and ITS-based phylogenetic trees. Although most leaf epidermal features show paraphyletic patterns when mapped onto the ITS tree, they are able to reveal the systematic placement of the taxa in subgenus *Cyclobalanopsis*. The epidermal features reported in the present study offer significant morphological resources that enable the identification of both herbarium foliage specimens and fossil leaves in subgenera *Cyclobalanopsis* and *Quercus*. However, future studies of the variation of leaf epidermal features at the intraspecific level and at different developmental stages of leaves of subgenus *Cyclobalanopsis* are needed to test the stability of these features and their significance to the taxonomy and systematics of this subgenus.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Trichome dimensions, arm number and length, and corresponding trichome base size measured in the present study on the leaf abaxial epidermis.