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LEAF ARCHITECTURE AND ITS SYSTEMATIC SIGNIFICANCE IN ACERACEAE FROM CHINA

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Abstract

Leaf architecture of 30 species representing 2 genera of Aceraceae in China was investigated for the first time. Within the 30 species, 10 species are found with an actinodromous venation pattern, while 20 species are found with a pinnate venation pattern. Within the 20 species with pinnate venation, 10 species are camptodromous, while the other 10 species are craspedodromous. Four types of leaf teeth are detected, viz. entire, toothed, lobed and partite. The secondary veins of most species are unbranched, except for *Acer cordatum*. Most species have obvious intersecondary veins, except for 4 species, i.e., *Dipteronia sinensis*, *D. dyerana*, *Acer davidii* and *A. maximowiczii*. All species have both reticulate and percurrent tertiary veins, except for *A. pentaphyllum,* which has only reticulate tertiary veins. All species are found with irregular areoles, except for *A. pentaphyllum* which is found to be regular. Veinlets are simple, branched or absent. A key to the genera and sections of Aceraceae mainly based on leaf architecture characters is presented.

Key words: Aceraceae, *Acer*, *Dipteronia,* Leaf architecture, Systematic significance.

Introduction

Aceraceae consists of 2 genera, i.e., *Acer* L. and *Dipteronia* Oliv., with about 200 species distributed worldwide and with about 150 species distributed in China. *Acer* L. is a larger genus, mostly deciduous or evergreen trees or shrubs, mainly distributed in north temperate Asia, Europe and America, and with only a few in the tropics. China is the modern distribution center of the genus *Acer*. The Chinese species account for more than 75% of the world species. They are distributed all over China. *Dipteronia* Oliv has only 2 species endemic to China, mainly in the West and southwest of China (Fang, 1981; Xu *et al*., 2008). There have been considerable controversies about the systematic position of Aceraceae in relation to the two families Sapindaceae and Hippocastanaceae (Radlkofer, 1931-1934; Xu, 1996; Tian & Li, 2004; Harrington *et al*., 2005; Buerki *et al*., 2009; Huang *et al*., 2013). Therefore, a renewed study of Aceraceae has taxonomic value.

Leaf architectural characteristics of plants are usually stable, which is of great importance in identifying plant fossils and for systematic taxonomy (Hickey, 1973, 1979; Dilcher, 1974; Hickey & Wolfe, 1975; Melville, 1976; Wilkinson, 1992; Buijsen, 1995; Roth-nebelsick *et al*., 2001; Cao *et al*., 2014). At the same time, leaf architectural morphology can be used as a basis for interfamily, intergeneric and interspecific classification, especially for the identification of species (Melville, 1976; Yu & Chen, 1986). Some scholars studied the leaf architectural and epidemal morphology of Sapindaceae, a related family of Aceraceae (Cao *et al*., 2014; Onuminya & Adediran, 2018). However, the leaf architecture of Aceraceae has not been thoroughly investigated so far. In this study, the leaf architectural characteristics of 30 species of Aceraceae are reported, and their systematic significance is discussed. The purpose of this study is to find the leaf architectural traits with systematic values, and to provide information for further studying the systematic relationship among species of Aceraceae.

Material and Methods

Most of the experimental materials for leaf architecture were taken from the herbarium specimens of the Southern China Botanical Garden, the Chinese Academy of Sciences (IBSC) additionally, some materials were collected in the field in Hengyang, Kunming and from the Royal Botanic Garden Edinburgh, and specimens were kept in Hengyang Normal University (HYNU). Materials selected for this study were mature leaves. The vouchers are listed in Table 1.

The method of investigating leaf venation followed that of Yu and Chen (1986). Mature leaves were selected, boiled in water for 20–30 min to soften and remove air from them, and then placed in 10%–20% NaOH at 70–80°C for 30-60 min. Rinsed in water, the epidermis and mesophyll were removed with a painting brush, then rinsed in running water for 6-8 h, and bleached in 20% sodium hypochlorite for 10–30 min, then rinsed in running water, stained in 5% methyl green or 1% safranin for 30 min, rinsed, dried and flattened. Leaf architecture was observed and photographed under a Shunyu stereoscopic microscope, and the whole leaves were photographed under a Cannon camera.

The terminology mainly follows that of Hickey (1973, 1979), Sun *et al*., (1997) and Ellis *et al*., (2009).

Table 1. Origin of materials.

Species	Locality	Voucher
Dipteronia sinensis Oliv.	Royal Botanic Garden Edinburgh	Cao 2016005 (HYNU)
D. dyerana Henry	Kunming Botanical Garden	Li 2018003 (HYNU)
Acer barbinerve Maxim.	Yichun, Heilongjiang	Haerbin Normal University 12994 (IBSC)
A. oblongum Wall. ex DC.	Luojin, Yongfu, Guangxi	Li Shuyang 6030 (IBSC)
A. coriaceifolium Levl.	Chaotian, Lingui, Guangxi	Chen Zhaozhou 31190 (IBSC)
A. laevigatum Wall.	Xingshan, Hubei	Hu Qiming 275 (IBSC)
A. sycopseoides Chun	Tianyang, Guangxi	Anonymous 15 (IBSC)
A. lucidum Metc.	Unknown	Huang Zhicheng 00075 (IBSC)
A. buergerianum Miq.	Campus of Wuhan University, Hubei	Liang Choufang 34559 (IBSC)
A. cordatum Pax	Longsheng, Guangxi	Guangfu forest region invest. team 870 (IBSC)
A. cinnamomifolium Hayata	Luojin, Yongfu, Guangxi	Li Shuyang 6034 (IBSC)
A. fabri Hance	Tongcheping, Yuanling, Hunan	Zhang Guicai *et al*., 478 (IBSC)
A. palmatum Thunb.	The campus of Heng. Nor. Univ., Hunan	Xiao Bing 090123
A. pubipalmatum Fang	Tianmushan, Zhejiang	Zhu Heqing 674 (IBSC)
A. mono Maxim.	Weichang, Hebei	Liu Xifu 5273 (IBSC)
A. cappadocicum Gled.	Laisu River, Fanxian, Sichuan	He Zhu, Zhou Zilin 14261 (IBSC)
A. davidii Franch.	Huangshan, Anhui	Anonymous 6056 (IBSC)
A. maximowiczii Pax	Kangding, Sichuan	Jiang Xingao 56344 (IBSC)
A. sinense Pax	Tiantangshan, Rongxian, Guangxi	Chen Shaoqing 9599 (IBSC)
A. wilsonii Rehder	Xingdoushan, Lichuan, Hubei	Tang Qingguo, Song Xianghou 435 (IBSC)
A. tutcheri Duthie	Longsheng, Guangxi	Anonymous 00559 (IBSC)
A. tetramerum Pax	Laisu, Nanchong, Sichuan	He Zhu, Zhou Zilin 14160 (IBSC)
A. ginnala Maxim.	Jiangsu	Zuo Jinglie 1282 (IBSC)
A. griseum (Franch.) Pax	Huashan, Shanxi	Zhang Zhiying 18234 (IBSC)
A. mandshuricum Maxim.	Jilin	F. H. Chen 410 (IBSC)
A. decandrum Merr.	Baoting, Hainan	Liu Xinqi 28204 (IBSC)
A. pilosum Maxim.	Qimingshan, Hebei	Wang Qiwu 62159 (IBSC)
A. pentaphyllum Diels	Yunnan	Yu Dejun 6711 (IBSC)
A. negundo Linn.	Tacheng, Xinjiang	Lin Yourun 74-1273 (IBSC)
A. henryi Pax	Tianzishan, Sangzhi, Hunan	Lin Qi 628 (IBSC)

Results

Leaf architecture of 30 species of Aceraceae in China was investigated, including all species of the genus *Dipteronia* and most sections of the genus *Acer* in China. Therefore, we can make a preliminary summary of the leaf morphological and structural characteristics of Aceraceae based on the results of this study. Leaves observed are often opposite, mostly simple and palmately lobed, sometimes pinnate or palmate compound, entire or toothed. The main veins in the taxa examined are either pinnate or actinodromous. Among the former type, most species are camptodromous, and some species are craspedodromous. Leaf morphological and architectural characters of the 30 species are shown in Table 2.

Actinodromous venation implies that three or more primary veins radiate from one point. Ten taxa studied belong to this type, i.e., *Acer mono, A. cappadocicum, A. palmatum, A. pubipalmatum, A. tutcheri, A. sinense, A. wilsonii, A. buergerianum, A. sycopseoides* and *A. pilosum* (Figs. 1C-F, 1H, 1I, 2A, 2B, 2J, 3E). Pinnate venation means that the blade has only one primary vein. The pinnate venation pattern includes two types, i.e., camptodromous and craspedodromous. Ten species are of the camptodromous type. The latter has two subtypes: brochidodromous and eucamptodromous. Brochidodromous means that the secondary veins are connected to each other, forming a series of obvious vein rings. Nine species studied adhere to this type, i.e., *A. cinnamomifolium, A. coriaceifolium, A. cordatum, A. fabri, A. laevigatum, A. lucidum, A. oblongum, A. pentaphyllum* and *A. henryi* (Figs. 2C-I, 3F, 3I). Eucamptodromous means that the secondary veins curve upwards, becoming progressively thinner and forming no vein rings. This type was only observed in *A. decandrum* (Fig. 3B). Ten species are craspedodromous, i.e., *Dipteronia sinensis, D. dyerana, A. ginnala, A. davidii, A. maximowiczii, A. barbinerve, A. tetramerum, A. griseum, A. mandshuricum* and *A. negundo* (Figs. 1A, 1B, 1G, 2K, 3A, 3C, 3D, 3G, 3H, 3J).

The primary vein is the largest vein originating from the petiole, going straight or being slightly curved. The primary veins of 12 species studied are moderately thickened, such as *Dipteronia sinensis* (Fig. 1A), *A. cappadocicum*, (Fig. 1D), *A. palmatum* (Fig. 1E), *A. sinense* (Fig. 1I), *A. cinnamomifolium* (Fig. 2C), *A. coriaceifolium* (Fig. 2D), *A. cordatum* (Fig. 2E), *A. oblongum* (Fig. 2I), *A. pilosum* (Fig. 3E) and *A. griseum* (Fig. 3G). Three species studied have stout primary veins, i.e., *D. dyerana* (Fig. 1B), *A. sycopseoides* (Fig. 2J) and *A. pentaphyllum* (Fig. 3F). The primary veins of the other 17 species are weakly developed, such as *A. ginnala* (Fig. 1G), *A. mandshuricum* (Fig. 3H) and *A. negundo* (Fig. 3J), etc.

The secondary veins originate from the primary veins and are weaker than the primary veins. They are curved or run straight, most of which are in a symmetrical pattern, 8-14 or 16-22 on each side. The secondary veins of most species are unbranched, except for *A. cordatum,* where branched secondary veins are observed (Fig. 2E, 4O).

Table 2. Comparison of Aceraceae based on leaf architectural and other morphological characters.

Genus/Section	Taxon	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
Dipteronia	*Dipteronia sinensis* Oliv	Cr	T	U	Var	-	Re, P	IR	Br	L
	Dipteronia dyerana Henry	Cr	T	U	Var	-	Re, P	IR	Br	L
Sect. *Platanoidea* Pax	*Acer mono* Maxim.	Ac	P	U	Var	+	Re, P	IR	S, Br	L
	A. cappadocicum Gled.	Ac	P	U	Var	+	Re, P	IR	S, Br	In
Sect. *Palmata* Pax	*A. palmatum* Thunb.	Ac	P	U	Var	+	Re, P	IR	Br	In
	A. pubipalmatum Fang	Ac	P	U	Var	+	Re, P	IR	Br	In
Sect. *Ginnala* Nakai	*A. ginnala* Maxim.	Cr	L	U	Con	+	Re, P	IR	Br	In
Sect. *Microcarpa* Pojark.	*A. tutcheri* Duthie	Ac	P	U	Var	+	Re, P	IR	Br	L
	A. sinense Pax	Ac	P	U	Var	+	Re, P	IR	Br	L
	A. wilsonii Rehder	Ac	P	U	Var	+	Re, P	IR	Br	In
Sect. *Integrifolia* Pax	*A. buergerianum* Miq.	Ac	L	U	Var	+	Re, P	IR	A, S	F
	A. cinnamomifolium Hayata	Br	En	U	Var	+	Re, P	IR	A, S	F
	A. coriaceifolium Levl.	Br	En	U	Var	+	Re, P	IR	A, S	F
	A. cordatum Pax	Br	T	B	Var	+	Re, P	IR	Br	In
	A. fabri Hance	Br	En	U	Var	+	Re, P	IR	Br	L
	A. laevigatum Wall.	Br	En	U	Var	+	Re, P	IR	Br	L
	A. lucidum Metc.	Br	En	U	Var	+	Re, P	IR	A, S	F
	A. oblongum Wall. ex DC.	Br	En	U	Con	+	Re, P	IR	A, S	F
	A. sycopseoides Chun	Ac	L	U	Var	+	Re, P	IR	A, S	F
Sect. *Macrantha* Pax	*A. davidii* Franch.	Cr	En	U	Var	-	Re, P	IR	A, S	In
	A. maximowiczii Pax	Cr	T	U	Var	-	Re, P	IR	Br	In
Sect. *Hyptiocarpa* Fang	*A. decandrum* Merr.	Eu	En	U	Con	+	Re, P	IR	A, S	F
Sect. *Arguta* Rehd.	*A.barbinerve* Maxim.	Cr	L	U	Var	+	Re, P	IR	S, Br	In
	A. tetramerum Pax	Cr	T	U	Var	+	Re, P	IR	Br	In
Sect. *Lithocarpa* Pax	*A. pilosum* Maxim.	Ac	P	U	Var	+	Re, P	IR	Br	In
Sect. *Pentaphylla* Hu et Cheng	*A. pentaphyllum* Diels	Br	En	U	Var	+	Re	R	A	L
Sect. *Trifoliata* Pax	*A. griseum* (Franch.) Pax	Cr	L, P	U	Con	+	Re, P	IR	A, S	In
	A. mandshuricum Maxim.	Cr	T	U	Var	+	Re, P	IR	A, S	In
Sect. *Cissifolia* Koidz.	*A. henryi* Pax	Br	En, T	U	Var	+	Re, P	IR	Br	In
Sect. *Negundo*	*A. negundo* Linn.	Cr	En, T	U	Con	+	Re, P	IR	S, Br	L

The divergence angle of secondary veins from the primary veins followed two distinct types in the examined species, namely, consistent and variable. The divergence angle of 6 species is consistent, i.e., *A. negundo* (Fig. 4L), *A. oblongum* (Fig. 4N), *A. ginnala* (Fig. 1G, 5D), *A. maximowiczii* (Fig. 5F), *A. decandrum* (Fig. 5I) and *A. griseum* (Fig. 5M). Variable types of divergence angle are found in 24 species, such as *A. buergerianum* (Fig. 4J), *A. sycopseoides* (Fig. 4K) and *A. Henryi* (Fig. 4M), etc.

Intersecondary veins usually originate from midveins and are distributed between secondary veins. They are (nearly) parallel to the secondary veins. They are weaker than secondary veins and stouter than tertiary veins. Obvious intersecondary veins are observed in 26 species,with only *Dipteronia sinensis* (4A), *D. dyerana* (4B), *A. davidii* (Fig. 5E) and *A. maximowiczii* (Fig. 5F) having non-obvious intersecondary veins.

Tertiary veins of *A. pentaphyllum* are randomly reticulate (Fig. 5N), while most species observed have reticulate and percurrent veins.

Areolas are well developed or consist of imperfectly closed meshes. There are 2 types of areolas observed in this study including regular and irregular areolas. Regular areolas imply that the sizes and shapes are relatively consistent. Only *A. pentaphyllum* has this type (Fig. 5N). Irregular areolas imply that the shapes are irregular, and the sizes vary widely from 1 to 2000 μm. Twenty nine species have this type, such as *A. negundo* (Fig. 4L), *A. henryi* (Fig. 4M) and *A. ginnala* (Fig. 5D), etc. The areolas are polygonal, quadrangular or irregular in shape.

The veinlets within the ultimate areolas are usually absent, simple and branched. Veinlets are absent in 11 species (Figs. 4J, 4K, 4N, 5A, 5B, 5C, 5E, 5I, 5L-N). Some veinlets of 14 species are simple (Figs. 4C, 4D, 4J-L, 4N, 5A-C, 5E, 5I, 5L, 5M, 5O). The veinlets of 18 species are 2-3 or more branched (Figs. 4A-I, 4M, 4O, 5D, 5F-H, 5J, 5K, 5O). Some veinlets of 13 species are single branched (Figs. 4C, 4D, 4J-L, 4N, 5A-C, 5E, 5I, 5L).

Three types of marginal ultimate venation were observed: (1) fimbriate: 7 species are of this type, i.e., *A. buergerianum* (Fig. 4J), *A. sycopseoides* (Fig. 4K), *A. oblongum* (Fig. 4N), *A. cinnamomifolium* (Fig. 5A), *A. Coriaceifolium* (Fig. 5B), *A. lucidum* (Fig. 5C) and *A. decandrum* (Fig. 5I). (2) looped: 9 species are of this type, i.e., *A. mono* (Fig. 4C), *A. sinense* (Fig. 4G), *A. Negundo* (Fig. 4L), *A. laevigatum* (Fig. 5G), *A. Fabri* (Fig. 5H) and *A. Pentaphyllum* (Fig. 5N). (3) incomplete: 14 species are of this type, i.e., *A. wilsonii* (Fig. 2A), *A. cappadocicum* (Fig. 4D), *A. palmatum* (Fig. 4E), *A. henryi* (Fig. 4M), *A. cordatum* (Fig. 4O), *A. ginnala* (Fig. 5D), *A. davidii* (Fig. 5E), *A. maximowiczii* (Fig. 5F), *A. tetramerum* (Fig. 5J), *A. pilosum* (Fig. 5K), *A. mandshuricum* (Fig. 5L) and *A. griseum* (Fig. 5M).

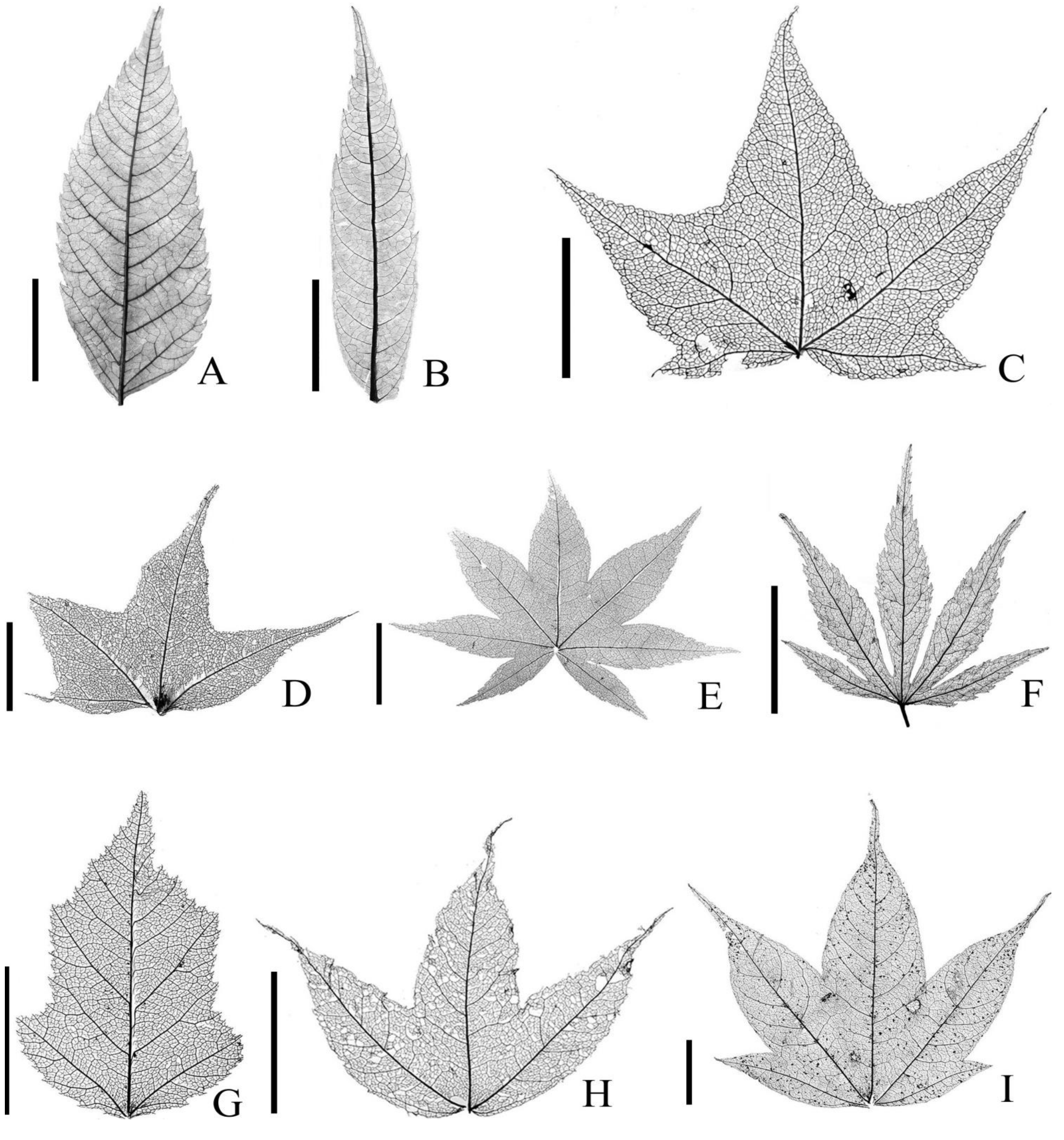

Fig. 1. Cleared leaves of species examined. A. *Dipteronia sinensis*; B. *D. dyerana* C. *Acer mono* Maxim.; D. *Acer cappadocicum* Gled.; E. *A. palmatum* Thunb.; F. *A. pubipalmatum*; G. *A. ginnala* Maxim.; H. *A. tutcheri* Duthie; I. *A. sinense* Pax (bar: A= 3cm; C, D=1cm; the others=2cm).

Notes: (1) Venation pattern: Ac, Actinodromous; Cr, Craspedodromous; Br, Brochidodromous; Eu, Eucamptodromous; (2) Tooth type: En, entire; T, toothed; L, lobed; P, parted; (3) Divergence of secondary veins: B, branched; U, unbranched; (4) Divergence angle of secondary veins from midveins: Con, consistent; Var, variable; (5) Intersecondary veins: +, present; －, absent or scarce; (6) Tertiary veins: Re, reticulate; P, percurrent; (7) Areoles: R, regular; IR, irregular; (8) Veinlets: S, simple; Br, branched; A, absent; (9) Marginal ultimate venation: F, fimbriate: L, looped; In, incomplete.

Four types of leaf margin, i.e., entire, toothed, lobed and parted, were observed. Eleven species are entire, such as *A. oblongum* (Fig. 4N), *A. coriaceifolium* (Fig. 5B) and *A. laevigatum* (Fig. 5G) etc. Eight species are toothed, i.e., *Dipteronia sinensis* (4A), *D. dyerana* (4B), *A. negundo* (Fig. 4L), *A. henry* (Fig. 4M), *A. mandshuricum* (Fig. 5L), *A. tetramerum* (Fig. 5J), *A. maximowiczii* (Fig. 5F) and *A. cordatum* (Fig. 4O). Five species are lobed, i.e., *A. ginnala* (Fig. 5D), *A. sycopseoides* (Fig. 4K), *A. buergerianum* (Fig. 4J), *A. tetramerum* (Fig. 5O) *and A. griseum* (Fig. 5M). Seven species are parted, i.e., *A. palmatum* (Fig. 4E), *A. cappadocicum* (Fig. 4D), *A. wilsonii* (Fig. 4H), *Acer mono*

(Fig. 4C), *A. pilosum* (Fig. 5K), *A. sinense* (Fig. 4g) and *A. pubipalmatum* (Fig. 4F). *A. griseum* (Fig. 5M) has both lobed and parted teeth types. *A. henryi* (Fig. 4M) and *A. negundo* (Fig. 4L) have both entire and toothed types.

Discussion

Aceraceae share a series of traits which makes it a natural group (Xu *et al*., 2008): leaves opposite, usually petiolate and estipulate, mostly simple and palmately lobed; flowers bisexual, polygamous or unisexual, actinomorphic; disk ringlike, extrastaminal, intrastaminal, or absent; ovary superior, compressed, usually 2-loculed; 2 ovules per locule, with only one ovule reaching maturity; style usually bifurcate, forming 2 reflexed stigmas; fruit a winged schizocarp, usually a double samara.

Leaf architecture of Aceraceae in China is relatively consistent: venation palmate or pinnate; the primary veins straight or slightly curved, usually weak (except in *A. sinense*, *A. davidii*, *A. maximowiczii* and *A. ginnala*), the secondary veins of most species wavy or slightly wavy; higher orders of veins generally up to 4th order, sometimes 5th order; intersecondary veins usually present; tertiary veins usually reticulate and percurrent; veinlets simple, or 2-3 or more branched, sometimes absent; marginal ultimate venation incomplete or looped, or fimbriate. Our results of leaf architecture characteristics also support the Aceraceae as a natural group.

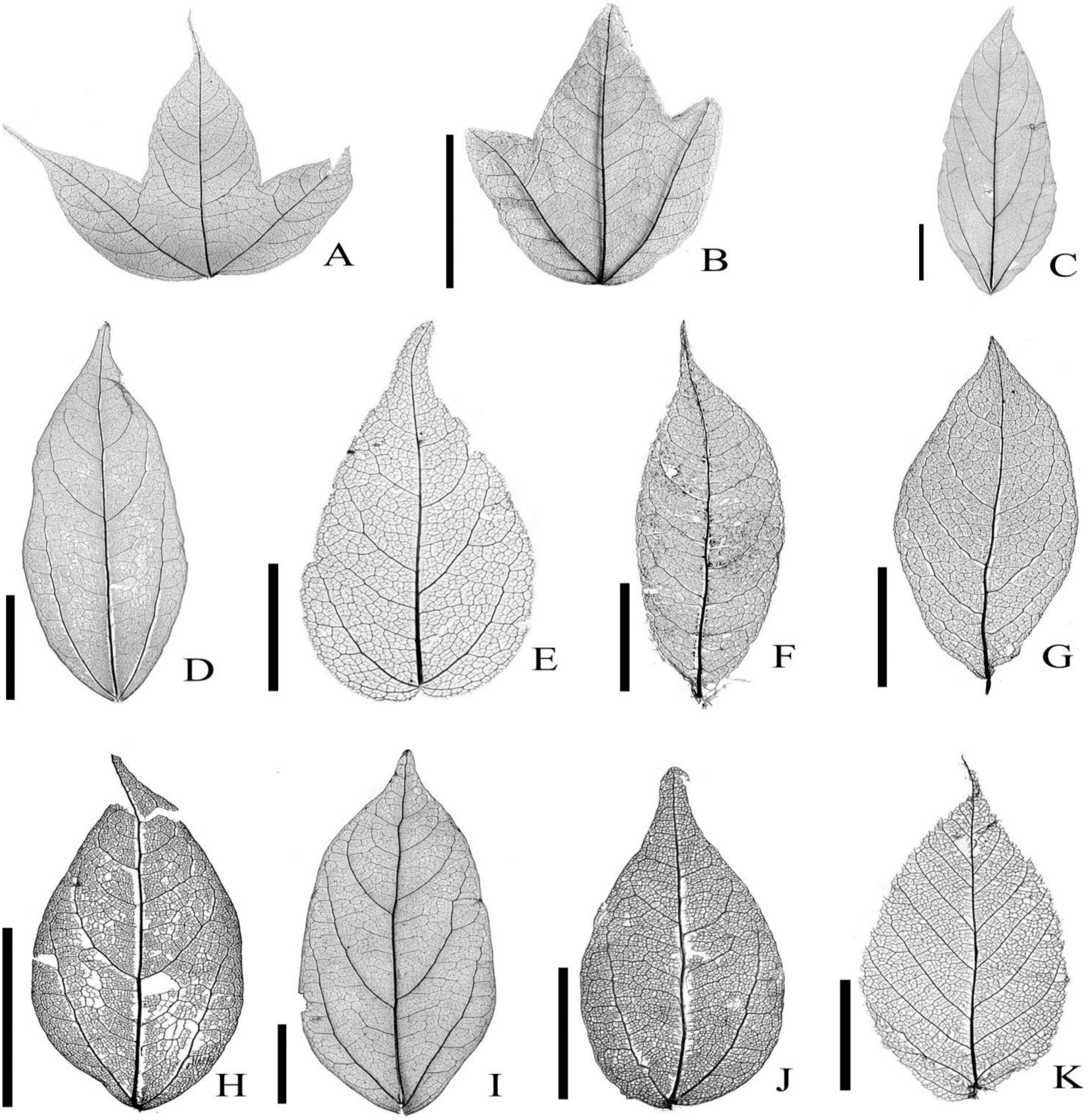

Fig. 2. Cleared leaves of species examined. A. *A. wilsoni* Rehder; B. *A. buergerianum* Miq.; C. *A. cinnamomifolium*; D. *A. coriaceifolium* Levl.; E. *A. cordatum* Pax; F. *A. fabri* Hance; G. *A. laevigatum* Wall.; H. *A. lucidum* Metc.; I. *A. oblongum* Wall. ex DC.; J. *A. sycopseoides* Chun; K. *A. davidii* Franch. (bar=2cm).

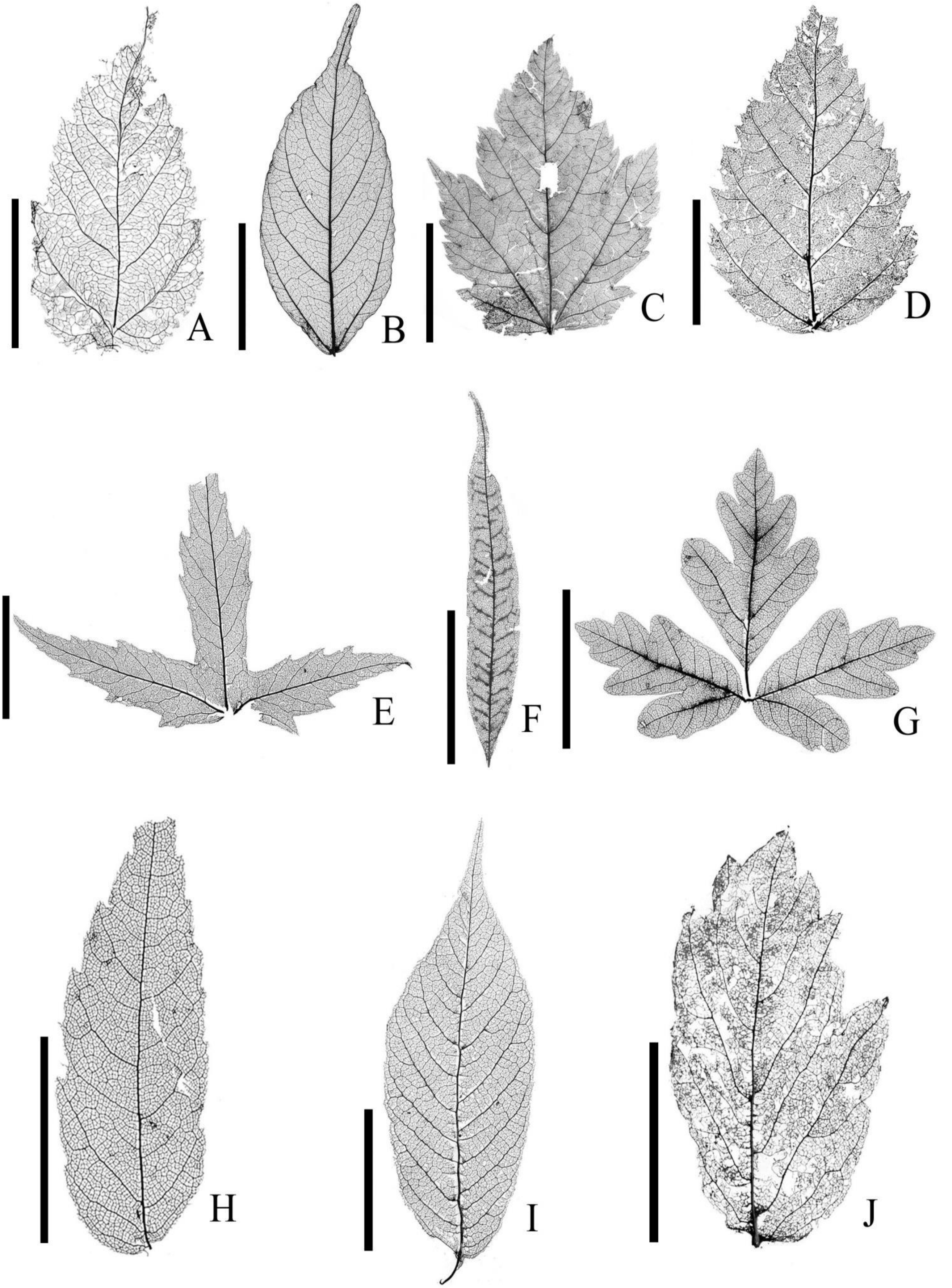

Fig. 3. Cleared leaves of species examined. A. *A. maximowiczii* Pax; B. *A. decandrum* Merr.; C. *Acer barbinerve*; D. *A. tetramerum* Pax.; E. *A. pilosum* Maxim.; F. *A. pentaphyllum* Diels; G. *A. griseum* (Franch.) Pax; H. *A. mandshuricum* Maxim.; I. *A. henryi* Pax; J. *A. negundo* Linn. (bar=2cm).

Dipteronia comprises two endemic species which are distributed in West and South West China. They can be easily distinguished from Acer by characters, such as smaller fruits, broad encircling winged samara, and pinnate leaves with 7-15 leaflets. Molecular phylogenetic analyses (Li *et al*., 2006, Renner *et al*., 2008) and morphological cladistic analyses (Tian & Li, 2004) support the separation of the genus *Dipteronia* from *Acer*. In this study, the leaf architectural characters of *Dipteronia* are also distinct from *Acer.* For example, leaves are imparipinnate and leaflets are papery. Leaf margin is remotely serrate with the teeth being acute, and the apex is acuminate or long acuminate. In addition, the venation pattern of *Dipteronia* is craspedodromous. Therefore, the evidence of leaf architecture in this study supports the division of Aceraceae into two genera, i.e., *Dipteronia* and *Acer*.

Leaf architectural characteristics of the two species in *Dipteronia* are quite consistent. In *Acer* of China, there are 2 subgenera and 15 sections, i.e., Subgen. *Acer*, including 13 sections, and Subgen. *Negundo*, including 2 sections. The leaf architectural characteristics are relatively consistent at subgeneric level, and could be used as key characters to distinguish the two subgenera.

Most species of Subgen. *Acer*, such as *A. sycopseoides*, *A. laevigatum*, *A. lucidum*, *A. coriaceifolium*, *A. tetramerum*, *A. oblongum*, *A. laevigatum*, *A. sinense*, *A. davidii*, *A. maximowiczii*, *A. mono*, *A. cordatum*, *A. palmatum*, etc, usually have simple leaves, rarely compound leaves with 3 or 5 leaflets. In this study, the venation pattern of 10 species observed is actinodromous, while that of the other 20 species is pinnate. Divergence of secondary veins is variable. Tertiary veins are reticulate and percurrent. Veinlets are usually branched. The architectural characteristics support the placement of these species into Subgen. *Acer*.

Acer negundo and *A. henryi* have following characteristics: pinnate compound leaves, leaflet blades ovate or elliptic, apex acuminate, base cuneate or broadly cuneate, margin entire or with 3-5 teeth, veinlets simple or branched, fimbrial veins absent. The architectural characteristics support the placement of these species into Subgen. *Negundo*.

In Flora Reipublicae Popularis Sinicae, Fang (1981) divided *Acer* into 15 sections, while Xu *et al*., (2008) divided Acer into 14 sections. In the treatment of Xu *et al*., (2008), Section *Microcarpa* was placed in Section *Palmata*, *A. pilosum* was separated from Section *Lithocarpa* and was treated as a separate section, and Section *Cissifolia* was placed into Section *Negundo*. We observed in this study that species in Section *Microcarpa* and Section *Palmata* share some similarities in their leaf architectures: leaf simple, parted, venation actinodromous, divergence angle of secondary veins from midveins variable, intersecondary veins present, tertiary veins reticulate or percurrent, areoles irregular, and veinlets branched. Thus, out results support the treatment of Xu *et al*., (2008) to merge Section *Microcarpa* with Section *Palmata*.

Section *Cissifolia* in China has only one species, and Section *Negundo* is a monotypic section. *A. henryi* and *A. negundo* are quite different in leaf architecture. In the former, the leaf is entire or sparsely toothed, with following characteristics: venation brochidodromous, divergence angle of secondary veins from midveins variable, veinlets branched, marginal ultimate venation incomplete. In the latter, the leaf is usually 3-5 parted, coarsely toothed or rarely entire, with following characteristics: venation craspedodromous, divergence angle of secondary veins from midveins consistent, veinlets simple or branched, marginal ultimate venation looped. The difference between the two species does not support the treatment of Xu *et al*., (2008) to place Section *Cissifolia* into Section *Negundo*.

Our study made it possible to create a key to the genera and sections observed in Aceraceae based on leaf architecture and other morphological characteristics:

1. Imparipinnate leaves with 9-15 leaflets; leaf margin acutely toothed .... *Dipteronia* Oliv.
1. Most single leaves, rarely palmate leaves or pinnate leaves with less than 7 leaflets; leaf margin entire, lobed, parted or partly toothed .... *Acer* Linn.
2. Leaves single, rarely compound, flowers polygamous or bisexual .... Subgen. *Acer*
3. Venation pattern actinodromous
4. Veinlets simple or branched once .... Sect. *Platanoidea*
4. Veinlets branched twice or more
5. Leaves 5-7 (or more) parted .... Sect. *Palmata*
5. Leaves usually 3-5 parted
6. Marginal ultimate venation incomplete .... Sect. *Lithocarpa*
6. Marginal ultimate venation looped .... Sect. *Microcarpa*
3. Venation pattern pinnate
7. Compound leaves
8. Leaves palmatifoliolate, 5(–9) leaflets; venation brochidodromous .... Sect. *Pentaphylla*
8. Leaves trifoliolate; venation craspedodromous .... Sect. *Trifoliata*
7. Simple leaves
9. Leaf margin toothed, lobed or parted
10. Divergence angle of secondary veins from midveins consistent .... Sect. *Ginnala*
10. Divergence angle of secondary veins from midveins variable .... Sect. *Arguta*
9. Leaf margin acutely entire
11. Intersecondary veins absent or scarce .... Sect. *Macrantha*
11. Intersecondary veins present
12. Venation eucamptodromous .... Sect. *Hyptiocarpa*
12. Venation actinodromous or brochidodromous .... Sect. *Integrifolia*
2. Pinnate compound leaves, flowers unisexual .... Subgen. *Negundo*
13. Marginal ultimate venation incomplete .... Sect. *Cissifolia*
13. Marginal ultimate venation looped .... Sect. *Negundo*

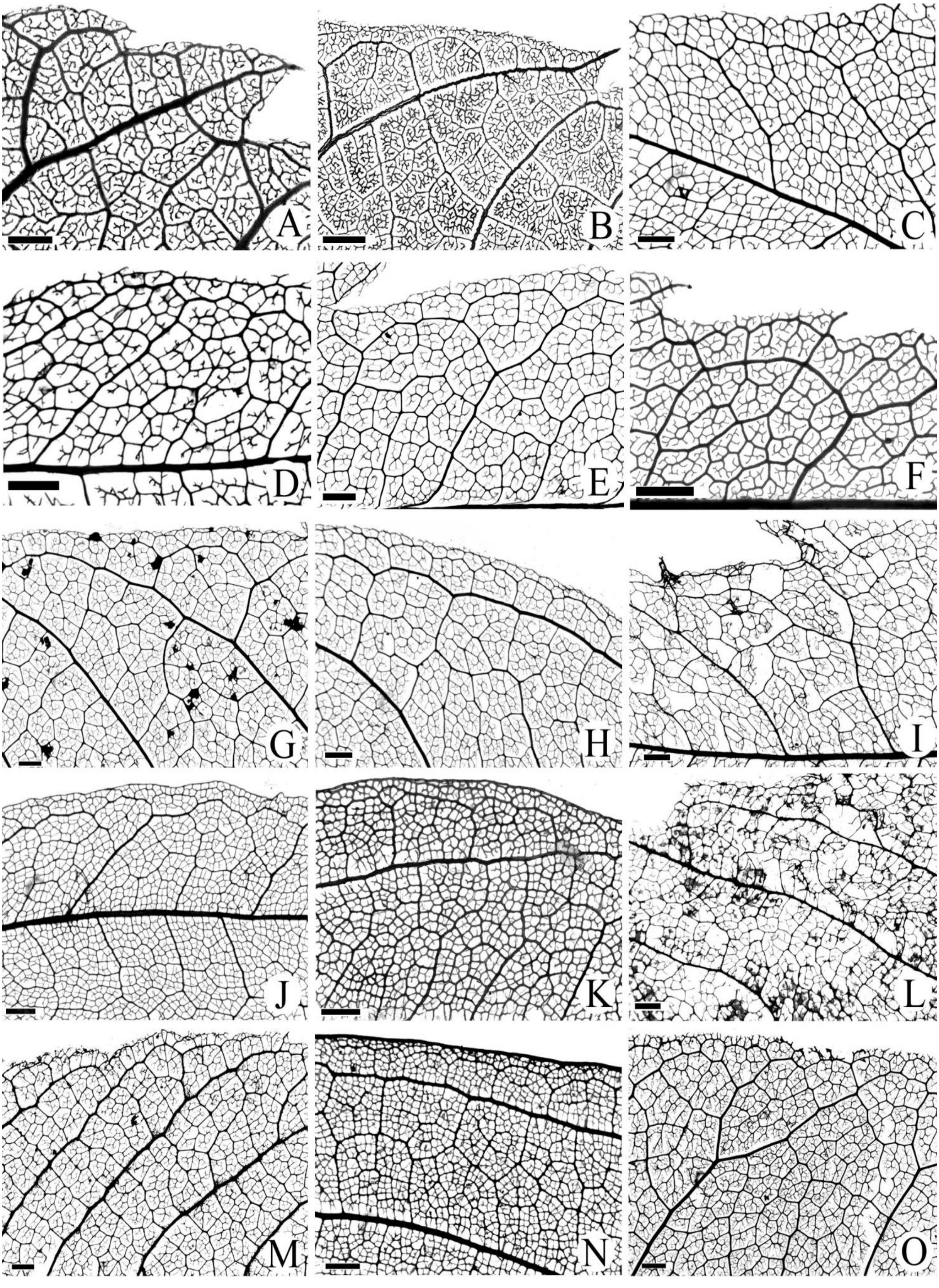

Fig. 4. Details of leaf architecture of species examined. A. *Dipteronia sinensis*; B. *D. dyerana*; C. *Acer mono* Maxim.; D. *A. cappadocicum* Gled.; E. *A. palmatum* Thunb.; F. *A. pubipalmatum* ; G. *A. sinense* Pax; H. *A. wilsonii* Rehder; I. *A. Tutcheri* Duthie; J. *A. buergerianum* Miq.; K. *A. sycopseoides* Chun; L. *A. negundo* Linn.; M. *A. henryi* Pax; N. *A. oblongum* Wall. ex DC.; O. *A. cordatum* Pax; (bar=1mm).

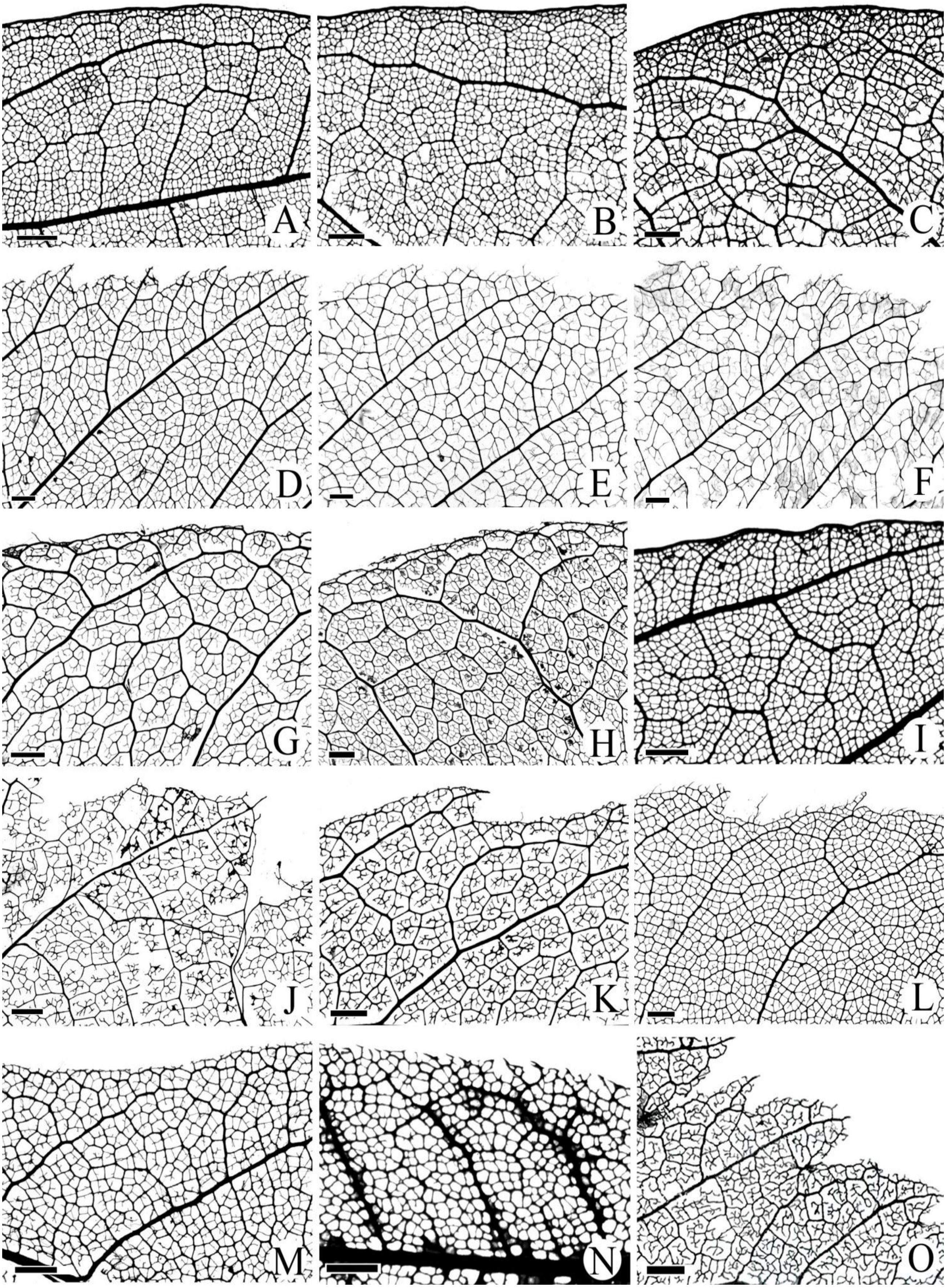

Fig. 5. Details of leaf architecture of species examined. A. *A. cinnamomifolium* ; B. *A. coriaceifolium* Levl.; C. *A. lucidum* Metc. N.; D. *A. ginnala* Maxim.; E. *A. davidii* Franch.; F. *A. maximowiczii* Pax; G. *A. laevigatum* Wall.; H. *A. fabri* Hance; I. *A. decandrum* Merr.; J. *A. tetramerum* Pax.; K. *A. pilosum* Maxim.; L. *A. mandshuricum* Maxim.; M. *A. griseum* (Franch.) Pax; N. *A. pentaphyllum* Diels; O. *A. barbinerve* (bar=1mm).

Conclusions

Leaf architectural characters provide useful taxonomic information in Aceraceae. The fourteen sections of *Acer* established by Xu *et al*., (2008) are well supported by the phenetic analysis of leaf architecture combined with other morphological characters, but the treatment of placing Section *Cissifolia* into Section *Negundo* seems to be inappropriate.

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References

Buerki, S., F. Forest, P. Acevedo-Rodríguez, M.W. Callmander, J.A. Nylander, M. Harrington, I. Sanmartín, P. Küpfer and N. Alvarez. 2009. Plastid and nuclear DNA markers reveal intricate relationships at subfamilial and tribal levels in the soapberry family (Sapindaceae). *Mol. Phylogenet Evol*., 51: 238-258.

Buijsen, J.R.M. 1995. Leaf anatomy of *Harpullia, Majidea,* and *Conchopetalum* (Sapindaceae). *Blumea,* 40(2): 345-361.

Cao, L.M., Z.X. Wang, M. Cao, J.H. Liu, Q. Lin and N.H. Xia. 2014. Leaf venation and its systematic significance in sapindaceae of China. *Plant Diversity Resour.,* 36(4): 419-432.

Dilcher, D.L. 1974. Approaches to the identification of angiosperm leaf remains. *Botanical Review,* 40: 1-157.

Ellis, B., D.C. Daly, L.J. Hickey, K.R. Johnson, J.D. Mitchell, P. Wilf and S.L. Wing. 2009. *Manual of Leaf Architecture* [M]. New York: Cornell University Press.

Fang, W.P. 1981. Aceraceae. In: flora reipublicae popularis sinicae. *Beijing: Science Press*, 46: 66-273.

Harrington, M.G., K.J. Edwards, S.A. Johnson, M.W. Chase and P.A. Gadek. 2005. Phylogenetic inference in Sapindaceae sensu lato using plastid matK and rbcL DNA sequences. *Syst. Bot.,* 30: 366-382.

Hickey, L.J. 1973. Classification of the architecture of dicotyledonous leaves. *Amer. J. Bot.*, 60: 17-33.

Hickey, L.J. 1979. A revised classification of the architecture of dicotyledonous leaves [M]. Metcalf C K, Chalk L. *Anatomy of the Dicotyledons* Vok. 1. Oxford: Clarendon Press, 25-39.

Hickey, L.J. and J.A. Wolfe. 1975. The bases of angiosperm phylogeny: vegetative morphology. *Ann. Mo. Bot. Gard.,* 62: 538-589.

Huang, Y.J., H. Zhu, W.Y. Chen and Z.K. Zhou. 2013. Intraspecific Variation in Samara Morphology of *Acer* and Its Implication in Fossil Identification. *Plant Diversity Resour.,* 35(3): 295-302.

Li, J.H., J.P. Yue and S. Shoup. 2006. Phylogenetics of *Acer* (Aceroideae, Sapindaceae) based on nucleotide sequences of two chloroplast non-coding regions. *Harvard Papers in Botany*, 11: 101-115.

Melville, R. 1976. The terminology of leaf architecture. *Taxon*, 25: 549-561.

Onuminya, T.O. and I.G. Adediran. 2018. Foliar epidermal morphology of some members of subfamily Dodonaeoideae-Sapindaceae. *Pak. J. Bot.*, 50(5): 1865-1869.

Radlkofer, L. 1931-1934. Sapindaceae. In A. Engler, *Das Pflanzenreich*, IV; 165. Leipig: Engelman.

Renner, S.S., G.W. Grimm, G.M. Schneeweiss, T.F. Stuessy and R.E. Ricklefs. 2008. Rooting and dating maples (*Acer*) with an uncorrelated rates molecular clock: implications for North American/Asian disjunctions. *Syst Biol.*, 57: 795-808.

Roth-Nebelsick, A., D. Uhl, V. Mosbrugger and H. Kerp. 2001. Evolution and function of leaf venation architecture: A Review. *Ann. Bot.,* 87: 553-566.

Sun, Q.G., S.Y. Song, Y.F. Wang and C.S. Li. 1997. Introduction to terminology of classification of dicotyledonous leaf architecture. *Acta. Phytotaxonomica Sininca,* 35(3): 275-288.

Tian, X. and D.Z. Li. 2004. Cladistic analysis of the Aceraceae based on morphological data set. *Acta Botanica Yunnanica*, 26(4): 387-397.

Wilkinson, H.P. 1992. Leaf anatomy of the Pittosporaceae. *Bot. J. Linn. Soc.,* 110: l-59.

Xu, T.Z. 1996 a. Samara shape of Aceraceae and its implications in systematics and evolution. *Guihaia*, 16(2): 109-122.

Xu, T.Z. 1996 b. A new system of the genus *Acer*. *Acta Botanica Yunnanica*, 18(3): 277-292.

Xu, T.Z., Chen Y.S. Piet, C. de Jong, Herman, J. Oterdoom and Chin-Sung Chang. 2008. Aceraceae. In: *Flora of China* (11): 515-553 (online).

Yu, C.H. and Z.L. Chen. 1986. Leaf architecture of the woody dicotyledons from South China I. Terminology and methods. *Acta. Botanica Austro Sinica*., 2: 83-97.

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