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Morphological Characters of Leaf Epidermis in Schisandraceae and Their Systematic Significance

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The leaf epidermis of 23 species belonging to 2 genera within Schisandraceae was investigated using light and scanning electron microscopy. Many characters of the leaf epidermis in Schisandraceae, such as shape of epidermal cells, type of stomata, and cuticular ornamentation, are usually constant within species and thus helpful for elucidating the relationship between and within genera. Leaf epidermal cells are usually irregular or polygonal in shape. The patterns of anticlinal walls are straight, sinuolate, sinuous or sinuate. The stomatal apparatus belong to paracytic or laterocytic type and the latter is subdivided into various subtypes based on the number and arrangement of subsidiary cells. Under scanning electron microscopy observation, the cuticular membrane is often striated, sometimes squamulate or granular; the inner margin of the outer stomatal rim is nearly smooth or denticulate. Evidences from shape of epidermal cells, patterns of cuticular intrusions between the ends of each guard cell of a pair and distribution of stomatal apparatuses support the viewpoint that *Kadsura* is more primitive than *Schisandra.* Study on leaf epidermis also shows that *Kadsura interior* deserves the rank of a distinct species and the treatment of the evergreen groups, including *S. propinqua* and *S. plena*, as distinct from the deciduous species of the genus is quite natural.

Keywords: Kadsura, leaf epidermis, morphology, *Schisandra*, Schisandraceae, systematic

Schisandraceae, along with Illiciaceae, belongs to the Illiciales (Hu, 1950; Cronquist, 1981), which are considered to be primitive dialycarpous angiosperms (Cronquist, 1981; Yang and Lin, 2005). Schisandraceae comprises two genera of scandent woody shrubs with unisexual flowers, viz. *Kadsura* and *Schisandra*, primarily occurring in tropical and warm temperate regions of East and Southeast Asia. There are 60 species belonging to 2 genera all over the Southeast of Asia and North America and 29 species found in China that is considered to be the diversification center (Law et al., 1996). The traditional division of Schisandraceae into two genera viz. *Kadsura* and *Schisandra* is essentially based on torus shape in the pistillate flowers and fruit: *Kadsura* species possess obovoid, subclavate or ellipsoid floral receptacles that remain short during fruit development so that the fruiting apocarps are closely appressed at maturity; in contrast, *Schisandra* species possess cylindrical or conical-terete floral receptacles that become greatly elongated during fruit development so that the fruiting apocarps are separated at maturity (Smith, 1947; Saunders, 1998, 2000; Hao et al., 2001).

In the past, various authors proposed classification systems for the family (Smith, 1947; Law et al., 1996; Saunders, 1997, 1998, 2000; Lin, 2000, 2002). Nonetheless, a consensus on the taxonomic treatment has not been reached until now. For example, a debate still exists on the relationship between *Schisandra* and *Kadsura*. Smith (1947) held the view that *Schisandra* was more primitive than *Kadsura*, but Law et al. (1996) and Saunders (1997) thought *Kadsura* was more primitive than *Schisandra*. While Sun (2000) proposed that *Schisandra* and *Kadsura* might originate from a common ancestor and have undergone parallel evolution along two different pathways; i.e. *Schisandra* and *Kadsura* have different evolutionary directions, based on pollen morphology. Yang and Lin (2005) raised that possibility with the data from morphology of leaf epidermis of 10 species in *Schisandra* and one species in *Kadsura*.

Leaf epidermal characters have been proved to be of great use not only in identifying the fossil remains of angiosperms but also in studying relationships between extant taxa (Baranova, 1972, 1983; Stace, 1984; Baranova, 1992; Yang and Lin, 2005). Although great contributions have been made on the study of leaf epidermis in Schisandraceae (Bailey and Nast, 1948; Jalan, 1962, 1965; Baranova, 1972, 1983; Wen et al., 2000), yet most of them contributed to description of the morphological features of leaf epidermis. The conclusion by Yang and Lin (2005) on the relationship between *Schisandra* and *Kadsura* is not convincing due to their insufficient

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sampling, that is to say, too few species were involved in leaf epidermal study. Thus, more detailed work, involving more species is required to test that conclusion and to establish a better systematic construction. Leaves of 23 species, belonging to 2 genera of Schisandraceae were examined mainly by means of LM and partially (abaxial epidermis) by SEM to provide materials for further research work on the relationship within this family. The delimitation of the genera *Kadsura* and *Schisandra* as well as recognition of species within them by Law et al. (1996) were adopted in this study.

MATERIALS AND METHODS

Leaf characters are constant and not impacted by whether the plant is dioecious or monoecious (Yang and Lin, 2005), so just one specimen for each species was sampled. Mature leaves were obtained from specimens in the Herbarium of Zhongshan University (SYS) and Herbarium of South China Botanical Garden, the Chinese Academy of Sciences (IBSC) (see appendix for voucher details). For LM, 3 pieces of mature leaves were boiled in water before being macerated in 10% NaClO or 2% Cr_2O_3. Pieces of leaf epidermis were stained with safranin-alcohol (50%), and then dehydrated in an alcohol series. After becoming transparent in xylene, they were sealed in neutral balsam. For SEM, leaves were washed with 95% alcohol before drying and then mounted on aluminium stubs. Coated with gold-silver alloy, they were examined and photographed under SEM (Hitachi S-520, Japan).

Table 1. The characters of leaf epidermis in Schisandraceae under LM.

Taxa	Adaxial epidermis		Abaxial epidermis				Figure
	Shape of cells	Pattern of anticlinal walls	Shape of cells	Pattern of anticlinal walls	Stomatotype (%)		
					Paracytic	Laterocytic	
Genus *Kadsura*							
K. ananosma	irr-pol	nearly str	irr-pol	nearly str	56.3	43.7	15, 30
K. coccinea	irregular	sinuous	irregular	sinuous	44.8	55.2	17
K. heteroclita	irregular	sinuate	irregular	sinuate	71.2	28.8	10
K. interior	irregular	sinuous	irregular	sinuous	40.8	59.2	7
K. longipedunculata	irregular	sinuolate	irregular	sinuolate	65.4	34.6	12
K. oblongifolia	irregular	sinuolate	irregular	sinuate	63.2	36.8	9, 20
K. scandens	irregular	sinuous	irregular	sinuous	57.5	42.5	
Genus *Schisandra*							
S. grandiflora	irregular	sinuolate	irr-pol	nearly str	51.2	48.8	11, 26
S. rubriflora	irr-pol	nearly str	irregular	sinuous	43.5	56.5	5, 21
S. incarnata	irr-pol	nearly str	irr-pol	sinuolate	45.7	54.3	3, 24
S. sphaerandra	irregular	sinuolate	irregular	sinuolate	18.5	81.5	13
S. heryi	irregular	sinuolate	irregular	sinuate	66.3	33.7	2, 14
S. pubescens	irregular	sinuous	irregular	sinuous	45.8	54.2	27, 8
S. wilsoniana	irregular	sinuolate	irregular	sinuolate	43.6	56.4	
S. sphenanthera	irr-pol	nearly str	irr-pol	nearly str	55.0	45.0	25
S. neglecta	irr-pol	nearly str	irr-pol	nearly str	49.3	50.7	22
S. viridis	irr-pol	nearly str	irr-pol	nearly str	7.9	92.1	4, 28
S. lancifolia	irregular	sinuolate	irregular	sinuolate	42.8	57.2	
S. micrantha	irr-pol	nearly str	irregular	sinuous	37.6	62.4	29, 16
S. bicolor	irregular	sinuolate	irregular	sinuous	9.6	90.4	
S. chinensis	irregular	sinuolate	irregular	sinuolate	34.1	65.9	23
S. propinqua	polygonal	straight	polygonal	straight	84.2	15.8	6, 18
S. plena	polygonal	straight	polygonal	straight	93.6	6.4	1, 19

irr-pol, irregularly polygonal; nearly str, nearly straight.

Table 2. The characters of abaxial epidermis of 23 species in Schisandraceae under SEM.

Taxa	Inner margin of outer stomatal rim	Cuticular membrane and wax ornamentation	Figures
Genus Kadsura			
K. ananosma	nearly smooth	striated	42
K. coccinea	denticulate	striated	41
K. heteroclite	denticulate	striated	35
K. interior	nearly smooth	granular	43
K. longipedunculata	nearly smooth	striated	38
K. oblongifolia	nearly smooth	striated; squamulate	47
K. scandens	nearly smooth	granular	
Genus *Schisandra*			
S. grandiflora	denticulate	striated	37
S. rubriflora	nearly smooth	striated, granular	33
S. incarnata	denticulate	squamulate	46
S. sphaerandra	denticulate	striated	
S. heryi	nearly smooth	striated	44
S. pubescens	denticulate	striated	
S. wilsoniana	nearly smooth	striated	36
S. sphenanthera	nearly smooth	striated	
S. neglecta	nearly smooth	striated	
S. viridis	denticulate	granular	
S. lancifolia	nearly smooth	striated	40
S. micrantha	nearly smooth	striated	34
S. bicolor	nearly smooth	striated, granular	48
S. chinensis	denticulate	striated; squamulate	45
S. propinqua	nearly smooth	striated	31,32
S. plena	nearly smooth	striated	39

RESULTS

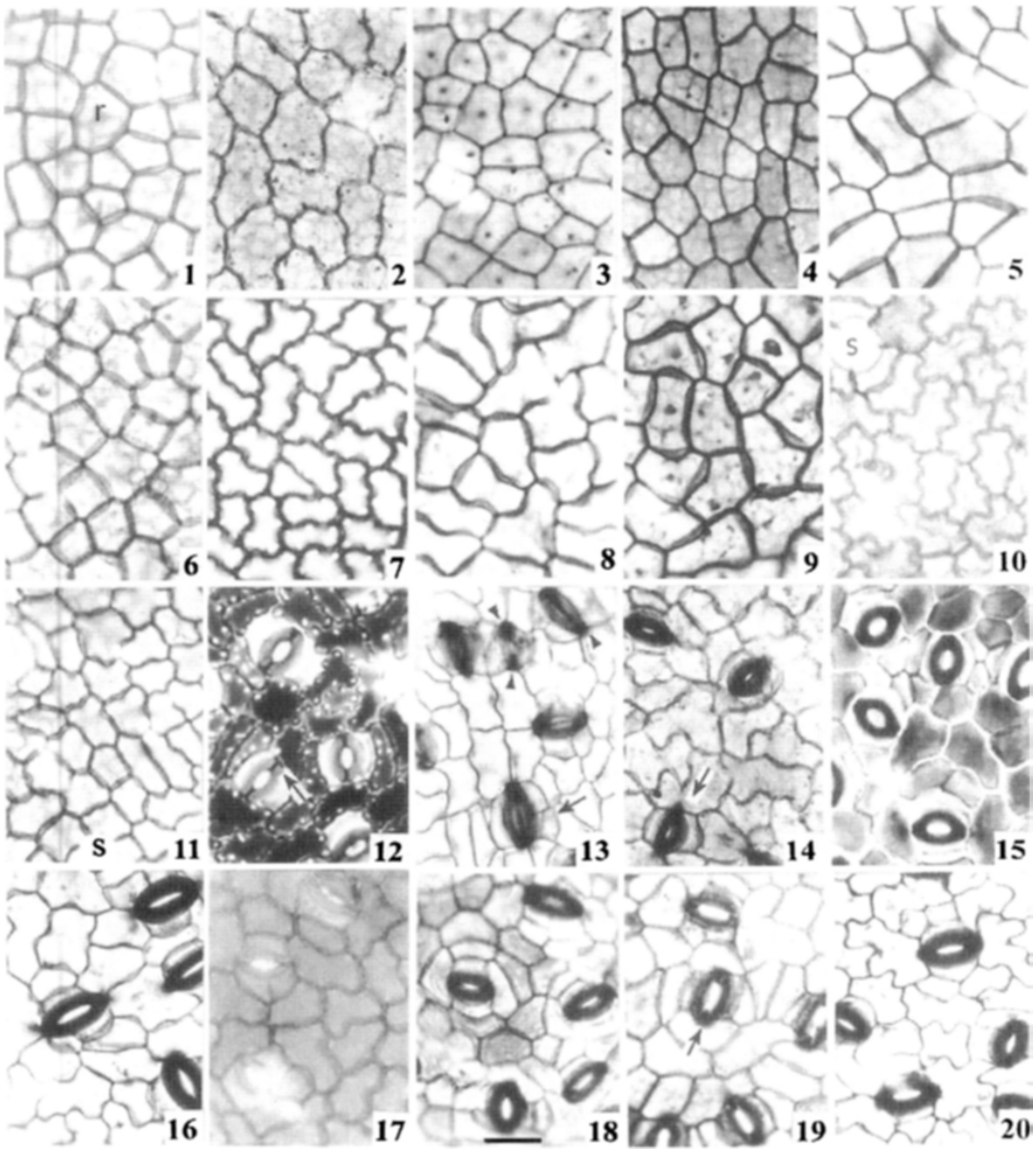
Stomatal Apparatus

Stomata were present on the abaxial epidermis for all species, but absent on the adaxial side for most species. Of all materials observed, only *Schisandra wilsoniana* exhibited stomata on both sides. The stomata on a single leaf conformed to 2 types, viz. paracytic (e.g., *S. henryi*, Fig. 14, shown by the arrow) and laterocytic. Determination of the extent of the variability, the predominant stomatotype and the proportion of other types was necessary, so that the stomatal characters could be properly correlated with other characters and useful for the purposes of classification (Baranova, 1992; Yang and Lin, 2005). Paracytic stomata were predominant in *S. plena* (93.6%) and *S. propinqua* (84.2%), whereas laterocytic stomata predominated in *S. viridis* (92.1%), *S. bicolor* (90.4%) and *S. sphaerandra* (81.5%). Various subtypes in laterocytic type were recognized based on the number and arrangement of subsidiary cells with subtypes "1+2" (one subsidiary cell on one side of the pair of guard cells and two on the other, e.g., *K. coccinea*, Fig. 17) and "2+2" (two on each side of the pair of guard cells, e.g., *S. pubescens*, Fig. 27) predominant. Occasionally, subtype "1+(1+ (1+1))" appeared as it was in the leaf epidermis of *S. sphaerandra* (Fig. 13, shown by the arrow). Under LM observation, the outlines of the pairs of guard cells were suborbiculate to elliptical. Under SEM observation, the guard cells were slightly elevated above the subsidiary cells. The outer stomatal rims, which were surrounded by various striaes, were almost at the same level with or slightly lower than the epidermis, obviously with beaks in the polar districts for the following species: *S. propinqua*, *K. hetero-*

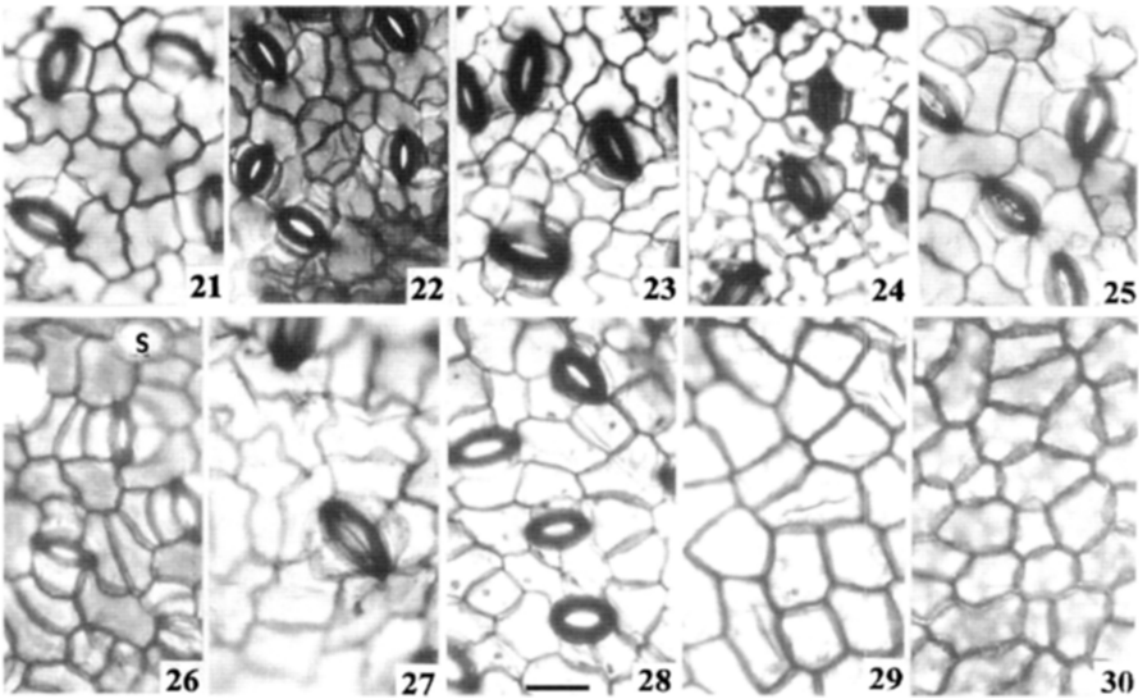
clita, *S. grandiflora*, *K. longipedunculata*, *S. plena*, *K. coccinea*, *K. interior*, *S. henryi*, and *S. incarnata*. The inner margin of outer stomatal rim was nearly smooth for some species (e.g., *S. propinqua*, Fig. 32) and denticulate for the others (e.g., *K. heteroclita*, Fig. 35) (Table 2).

Shape of Leaf Epidermal Cells and Patterns of Anticlinal Walls

Anticlinal walls in most species inclined, namely they formed obtuse or acute angles with the leaf surface. Three types of leaf epidermal cells were recog-



Figures 1-30. LM photographs of shape of leaf epidermal cells, patterns of anticlinal wall and types of stomatal apparatus (1-11, 29-30. adaxial epidermis; 12-28. abaxial epidermis). Scale bar = 40 μM. 1, *S. plena* (note a rosette-cell arrangement (r)); 2, *S. henryi*; 3, *S. incarnata*; 4, *S. viridis*; 5, *S. rubriflora*; 6, *S. propinqua*; 7, *K. interior*; 8, *S. pubescens*; 9, *K. oblongifolia*; 10, *K. heteroclita* (note a secretory cell (s)); 11, *S. grandiflora* (note a secretory cell (s)); 12, *K. longipedunculata*; 13, *S. sphaerandra*; 14, *S. henryi*; 15, *K. ananosma*; 16, *S. micrantha*; 17, *K. coccinea*; 18, *S. propinqua*; 19, *S. plena*; 20, *K. oblongifolia*.



Figures 1-30. Continued. 21, *S. rubriflora*; 22, *S. neglecta*; 23, *S. chinensis*; 24, *S. incarnata*; 25, *S. sphenanthera*; 26, *S.grandiflora*; 27, *S. pubescens*; 28, *S. viridis*; 29, *S. micrantha*; 30, *K. ananosma*.

nized according to their shape: (1) polygonal cells, the anticlinal wall was straight, e.g., *S. plena* (Fig. 1); (2) irregular cells, the anticlinal wall was sinuolate (*Kadsura oblongifolia*, Fig. 9), sinuous (*K. interior*, Fig. 7) and sinuate (*K. heteroclita*, Fig. 10); (3) irregularly polygonal cells, the anticlinal wall was somewhat straight or sinuolate in terms of Yang et al. (2000), e.g., *S. incarnata* (Fig. 3). It was regarded as a transition from type polygonal to type irregular (Yang et al., 2000). Generally speaking, to the same species, cells in the abaxial and adaxial epidermis were of the same shape. Two examples were *S. propinqua* (Fig. 6, 18) and *S. plena* (Fig. 1, 19). In these two species, abaxial and adaxial epidermal cells were all polygonal and anticlinal walls were all straight. Only to few species, the shape of adaxial epidermal cells was different from that of abaxial ones. For example, anticlinal wall was sinuolate in the adaxial epidermis of *K. oblongifolia*, whereas sinuate in the abaxial epidermis (Fig. 9, 20). Listed in table 1 are shape of cells, patterns of anticlinal walls and types of stomatal apparatus of 23 examined species.

Cuticular Intrusions

Cuticular intrusions known as 'T' pieces between the ends of each guard cell of a pair were found in *K. longipedunculata* (Fig. 12, shown by the arrow). Cuticular intrusions were sometimes reduced to a rod or bar, e.g., *S. plena* (Fig. 19, shown by the arrow). A cuticular intrusion as a clump in the polar district of the stomata was observed in *S. sphaerandra* (Fig. 13, shown by the arrow head).

Secretory Cells and Rosette-Cell Arrangements

Secretory cells were found in abaxial epidermis of some species and on adaxial side of other species [e.g., *K. heteroclita*, *S. grandiflora* (Fig. 10, 11), "s" denotes a secretory cell]. A special structure named as a rosette-cell arrangement by Hong et al. (2001), where an epidermal cell was surrounded by 6-8 cells radially, was also discerned in *S. plena* (Fig. 1, r denotes a rosette-cell arrangement).

Cuticular Membrane and Wax Ornamentation

Under SEM observation, the cuticular membrane of the leaf epidermis was often striated, sometimes squamulate or granular. The inner margin of outer stomatal rim was nearly smooth or denticulate (Table 2). Some species had only cuticular striaes, e.g., *K. longipedunculata* and *S. plena*. (Fig. 38, 39); some had cuticular striaes and wax granules, e.g., *S. rubri-*

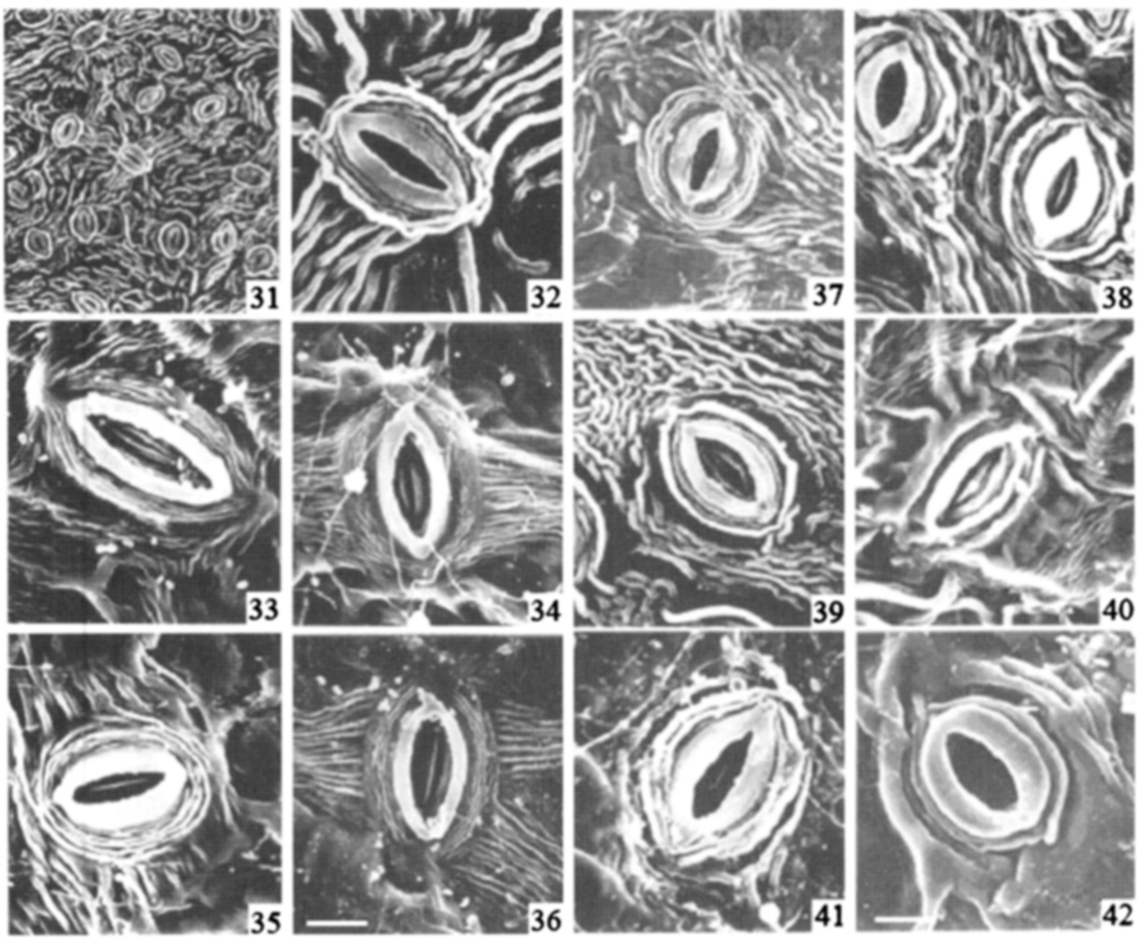
flora (Fig. 33); some had only wax squamules, e.g., *S. incarnata* (Fig. 46); some had cuticular striaes and wax squamules, e.g., *S. chinensis* and *K. oblongifolia* (Fig. 45, 47).

DISCUSSION

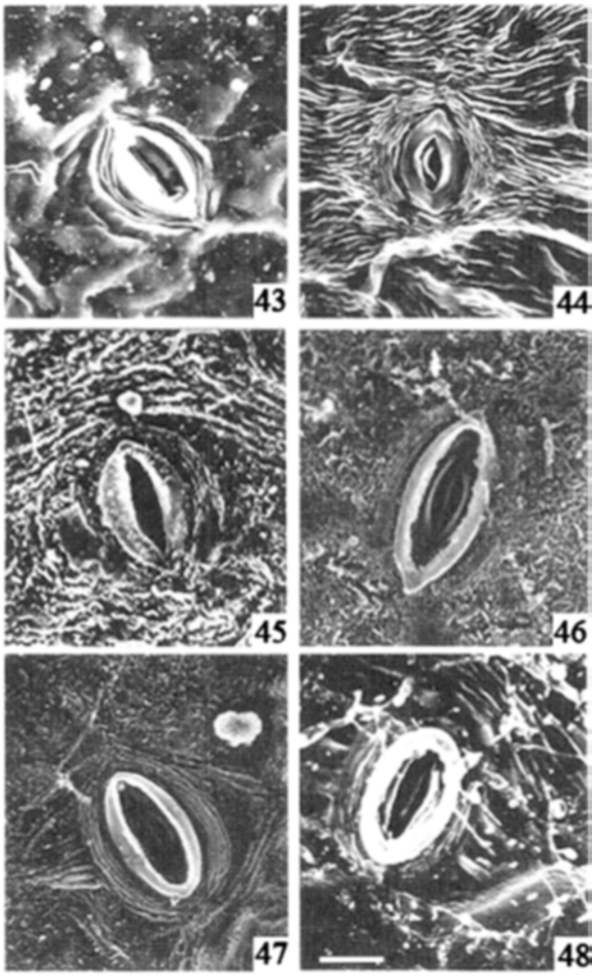
Wen et al. (2000) and Yang and Lin (2005) reported some characteristics of leaf epidermis of genus *Schisandra* under LM and SEM. Their results are similar to this report in respect to shape of epidermal cells, patterns of anticlinal walls, types of stomata, secretory cells, cuticular membrane and wax ornamentation. The present investigation yielded a few new findings and offered some meaningful results.

In Illiciales, irregular epidermal cells, cuticular intrusions known as 'T' pieces between the ends of each guard cell of a pair and absence of stomatal apparatus in the adaxial epidermis are primitive, while polygonal cells, that cuticular intrusions are reduced to a rod or bar, and presence of stomatal apparatus in the adaxial epidermis are derived (Wen et al., 2000). In this survey, epidermal cells are usually irregular in *Kadsura* (mentioned above). Only in *Schisandra*, do polygonal cells occur (*S. propinqua* and *S. plena*). Cuticular intrusions known as 'T' pieces occur in *Kadsura* (*K. longipedunculata*), whilst cuticular intrusions are reduced to a rod or bar in *Schisandra* (*S. propinqua* and *S. plena*). *S. wilsoniana*, the only species which exhibits stomata in the adaxial epidermis, falls into *Schisandra*. All these support the viewpoint that *Kadsura* is more primitive than *Schisandra* (Law et al., 1996; Saunders, 1997).

Concerning *K. interior*, different scholars expressed different approaches. Law et al. (1996) referred to it as a distinct species, whereas Lin (2002) considered it to be a synonym of *K. heteroclita*. While comparing, I



Figures 31-48. Characters of the leaf epidermis under SEM. Scale bar = 100 μM in Fig. 31, and scale bar = 20 μM in the others. 31-32, *S. propinqua*; 33, *S. rubriflora*; 34, *S. micrantha*; 35, *K. heteroclita*; 36, *S. wilsoniana*; 37, *S. grandiflora*; 38, *K. longipedunculata*; 39, *S. plena*; 40, *S. lancifolia*; 41, *K. coccinea*; 42, *K. ananosma*.



Figures 31-48. Continued. 43, *K. interior*; 44, *S. henryi*; 45, *S. chinensis*; 46, *S. incarnata*; 47, *K. oblongifolia*; 48, *S. bicolor*.

found that *K. interior* differs from *K. heteroclita* in the following aspects: Under LM observation, there were secretory cells in adaxial epidermis of *K. heteroclita* but not in *K. interior* (Fig. 7, 10). Under SEM observation, the beak in the polar district of outer stomatal rim in *K. interior* was much longer than that of *K. heteroclita*; the inner margin of outer stomatal rim of the former was nearly smooth, the latter denticulate; cuticular membrane of the former was granular, the latter striated (Fig. 35, 43). At this point, I would claim that *K. interior* deserves the rank of a distinctive species, thus approving of the treatment of Law et al. (1996).

Saunders' sect. *Sphaerostema*, namely the evergreen group, comprising *S. propinqua* and *S. plena*, is justified by evidence from seed surface features and molecular data (Hao et al., 2001; Sun, 2002). Morphologically, the plants in this section are evergreen; leaf laminae are chartaceous to subcoriaceous; flowers are solitary, in clusters, raceme or panicle; receptacles are carneous and inflated, globular or obovoid (male flowers); torus is not thickened, and peduncle is not elongated as fruits mature (female flower); testa is reticulate (Yang and Lin, 2005). Under LM observation, the epidermal cells are polygonal and paracytic stomata predominate for the two species (Fig. 1, 6, 18, 19; Table 1). Under SEM observation, for either of them, the inner margin of outer stomatal rim is nearly smooth, cuticular membrane and wax ornamentation striated (Fig. 31, 32, 39). Evidences from the macromorphology and leaf epidermal features indicate that the two species are closely related. Therefore the treatment of the evergreen groups as distinct from the deciduous species of the genus is quite natural. It seems unreasonable to put *S. propinqua* and *S. plena* in two different subgenera (subgenus *Sphaerostema* and subgenus *Plenischischisandra*) (Law et al., 1996).

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Appendix. Origin and accession number for specimens utilized for study on leaf epidermis. All voucher specimens are deposited at IBSC or SYS.

K. ananosma Kerr, Hunan *Pei-Xiang Tan 63228* (IBSC); *K. coccinea* (Lem.) A.C. Smith, Luofu mount, Guangdong *N.K.CHUN 41395* (SYS); *K. heteroclita* (Roxb.) Craib, Longsheng county, Guangxi *Guang-Fu forest district team 00601* (SYS); *K. interior* A.C. Smith, Yunnan *Jing-Sheng Yang 4255* (IBSC); *K. longipedunculata* Finet et Gagnep., Ruyuan county, Guangdong *section B, Class72-143* (SYS); *K. oblongifolia* Merr., No.157 Hospital *Sheng-Fang Lan 2655* (SYS); *K. scandens* Bl., Fan shiu shan, Wung Yuen District *Lau. S.K. 2725* (SYS); *S. grandiflora* (Wall.) Hook. f.et Thoms., Omei mountain *Plant Expedition, Dept. of Bio, Sichuan University-53054* (SYS); *S. rubriflora* (Franch.) Reld. et Wils, Sichuan *K.L. Chu 2017* (IBSC); *S. incarnata* Stapf, Baokang, Hubei *Ren-Huang Huang 2787* (IBSC); *S. sphaerandra* Stapf, Yunnan *Han-Chen Wang 3625* (IBSC); *S. henryi* Clarke., Guangxi *Chou-Fen Liang 30255* (SYS); *S. pubescens* Hemsl. et Wils., Omei mountain *Guang-Hui Yang 56707* (SYS); *S. wilsoniana* A.C. Smith, HERB. HORT. REG. BOT. EDIN *GEORGE FORREST, y622* (SYS); *S. sphenanthera* Rehd et Wils., Yinna mount, Mei county *Tsang W.T.21423* (SYS); *S. neglecta* A.C. Smith, Lanping county, Yunnan *H.T. Tsai 57594A* (IBSC); *S. viridis* A.C. Smith, Guangdong *Xian-Rui Luo 1420* (IBSC); *S. lancifolia* (Reld. et Wils) A.C. Smith, Yunnan *Wan-Chao Yang 89038* (IBSC); *S. micrantha* A.C. Smith, Yunnan *Shen-E Liu 16309* (IBSC); *S. bicolor Cheng*, Prov. Ohmi mt. Hirasan *Z. Jashizo, s.n.* (SYS). *S. chinensis* (Turcz.) Baill, Shansi *T. Tang 972* (SYS); *S. propinqua* (Wall.) Baill., Zhongshan University *Hung-Ta Chang 6494* (SYS); *S. plena* A.C. Smith, Menglun Huiwa *Hua Zhu 160104* (SYS).