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RESEARCH ARTICLE

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Comparative morphology on leaves of *Daphniphyllum* (*Daphniphyllaceae*)

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Key words

Daphniphyllaceae
Daphniphyllum
epidermis
leaf anatomy
Lunata
stomata

Abstract A comparative anatomical study on the leaves of nine out of 29 species of the genus *Daphniphyllum* was performed to seek support for the present infrageneric classification. *Daphniphyllum* is composed of two sections, *Lunata* (with one subsection *Lunata*) and *Daphniphyllum* (with two subsections, *Daphniphyllum* and *Staminodia*). The glabrous leaves with brachyparacytic stomata appear in all species in this study; hemiparacytic, laterocytic or anomocytic stomata occur in some taxa. Two (out of three) species of section *Lunata* show irregular epidermal cells with undulate anticlinal walls on both surfaces and hemiparacytic stomata. Of section *Daphniphyllum* seven (out of 26) species were sampled; they have curved, straight or undulate anticlinal cell walls and laterocytic or anomocytic stomata. The anatomical features found in this study are useful for identification on the specific level, but there is no support for the current infrasectional classification of section *Daphniphyllum*; further study on section *Daphniphyllum* is necessary.

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INTRODUCTION

Daphniphyllaceae is a monogeneric family distributed from tropical to subtropical Asia, including East Asia, Southeast Asia, Nepal, India, and Sri Lanka between about 46° N and 10° S and 75° E and 150° E (Rosenthal 1919, Huang 1965, 1966, 1996, 1997). *Daphniphyllum* comprises about 30 species (Ming 1980, Ming & Kubitzki 2008) of evergreen trees or shrubs with simple, entire, alternate to subverticillate leaves. This genus was established by Blume (1826). The monographic study of *Daphniphyllum* was initiated by Müller in 1869, who distinguished 13 species. Rosenthal (1916, 1919) finished a monograph of *Daphniphyllum* with 24 recognized species and he divided the genus into two groups based on the presence/absence of papillae on the abaxial leaf surface. Around fifty years later, Huang (1965, 1966) produced a second monograph of *Daphniphyllum*. He recognized nine species with 21 subspecies and around 25 varieties based on morphological characters of styles and sepals. Huang classified this genus into three sections: *Lunata* (3 species), *Staminodia* (2 species) and *Daphniphyllum* (4 species); and sect. *Daphniphyllum* was further subdivided into three subsections, *Longicalycifera* (1 species), *Unicalycifera* (2 species) and *Daphniphyllum* (1 species). However, 30 years later, Huang (1996, 1997) modified his classification and divided the genus into two sections, *Lunata* and *Daphniphyllum*, and he treated previous sect. *Staminodia* as a subsection of sect. *Daphniphyllum*. He also reduced previous subsections, *Longicalycifera* and *Unicalycifera*, to series under subsect. *Daphniphyllum* (Huang 1996, 1997) (Fig. 1).

Textures and shapes of the leaves are variable in *Daphniphyllum* (Croizat & Metcalf 1941, Huang 1965). The staminate flowers and drupes only provided limited characters for species identification, also in combination with leaf morphology (Huang 1965). Leaf anatomical features proved to be of great value in many taxa not only in identifying species, but also in understanding relationships between taxa (Baas 1981, Pan et al. 1990, Mentink & Baas 1992, Kong 2001, Sheue et al. 2003, Gonzalez et al. 2004, Kocsis et al. 2004, Carpenter 2005, 2006). The leaf anatomical study of *Daphniphyllum* was extremely meager up to now. Metcalfe & Chalk (1988, 1989) described paracytic stomata, clusters of crystals and papillae on the abaxial surface for *Daphniphyllum*. The stomatal complex of four species of *Daphniphyllum*, *D. chartaceum, D. macropodum, D. triangulatum* and *D. yunnanense*, was studied by Zhang & Lu (1989). They showed that the paracytic type occurs in all four species. Huang (1965) described the leaf anatomy for five taxa, *D. calycinum*, *D. gracile*, *D. glaucescens* subsp. *oldhamii*, *D. himalaense* subsp. *angustifolium* and *D. himalaense* subsp. *macropodum,* and mentioned that "the upper, lower epidermis, sponge and palisade cells are different within species level".

The purpose of this comparative study is to provide morphological and anatomical characters, which may be helpful in species identification and can be used to support the present classification of the genus.

MATERIALS AND METHODS

Of the 29 *Daphniphyllum* species, two (out of three) species, *D. calycinum* and *D. majus*, were sampled to represent sect. *Lunata*; the other seven species (out of 26) were selected to represent sect. *Daphniphyllum* (Table 1). For two species dried leaf fragments of herbarium specimens were used. Fresh and desiccated materials of the other species were collected in the field in China, Japan, the Philippines and Taiwan. Vouchers are deposited in the herbarium of SYSU.

Fresh leaf pieces were fixed in FPGA (formalin : propionic acid : glycerol : 95 % ethanol : distilled water = 5 : 5 : 15 : 35 : 40 in volume). Desiccated material was dipped in water and then transferred to FPGA. Parts of leaf samples were dehydrated by ethanol series and then embedded in paraffin for microtome section. Sections of 8–12 µm thickness were cut by a Leitz 1512 rotary microtome and stained with 1 % Safranin O and 0.5 % fast green. The apex, middle and base parts of leaves

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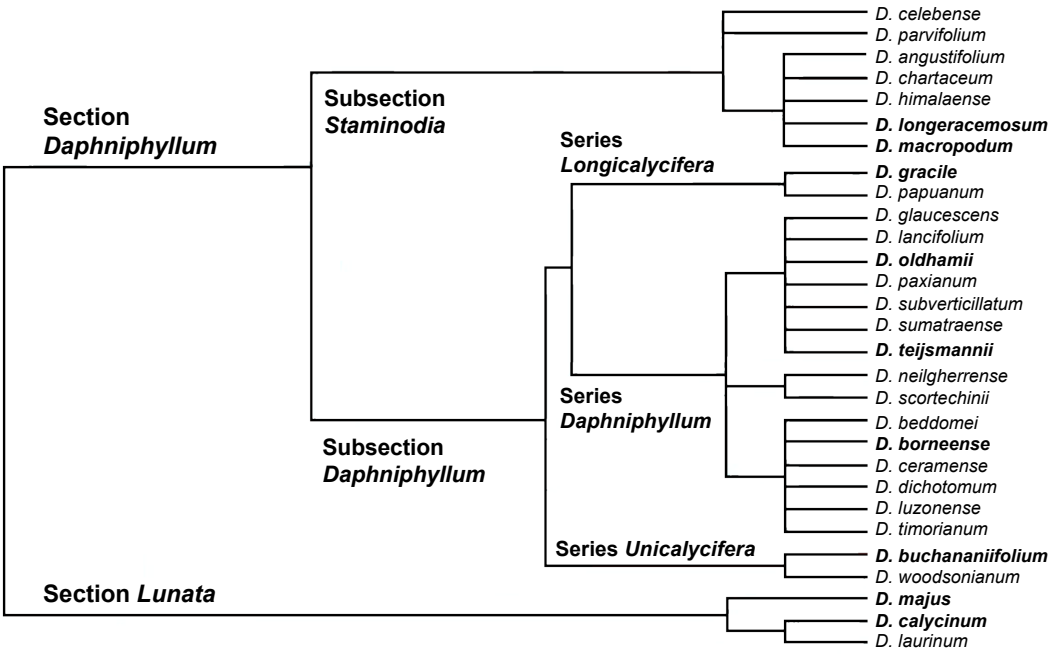

Fig. 1 Diagram showing the classification of *Daphniphyllum* based on Huang (1965, 1996, 1997), Ming & Kubitzki (2008) and Hatusima (1971). Studied species are indicated in **bold**.

were cleared with 3 % sodium hydroxide at 40 °C for 5–14 days and stained with 1 % Safranin O. Paraffin sections and cleared leaves were observed and photographed with a Leica DME light microscope and a Nikon D70s digital camera. The mean length of stomatal guard cells was measured from each specimen with 40 replications.

Terminology follows Dilcher (1974) except for the term 'laterocytic stomata' (Carpenter 2005) that was used to describe the unequal parts of asymmetric stomata.

RESULTS

Leaf characteristics of the epidermis and transverse sections of *Daphniphyllum* are summarized in Table 2. Palisade tissue, stomatal and epidermal features of all studied taxa appear to be constant on the species level. Typical leaf morphological characters for sections, subsections and series are summarized in Table 3.

Palisade and spongy tissues

The leaf structure of *Daphniphyllum* is dorsiventral. The nine species can be divided into two groups on the basis of cell form and arrangement of palisade tissues (Table 2). One group shows columnar and compactly arranged palisade cells (Fig. 2c, f–h). The other group shows loosely arranged conical to round palisade cells (Fig. 2a, b, d, e). The first group comprises species in subsect. *Daphniphyllum* (*D. borneense, D. buchananiifolium*, *D. gracile*, *D. oldhamii* and *D. teijsmannii*); the second group contains sect. *Lunata* (*D. calycinum*, *D. majus*) and subsect. *Staminodia* (*D. longeracemosum* and *D. macropodum*). The palisade cells are 1-layered in most species of the second group except for *D. macropodum* with three layers.

Table 1 Leaf materials of *Daphniphyllum* used in this study. The classification follows Huang (1996, 1997), Ming & Kubitzki (2008) and Hatusima (1971).

Classification	Taxon	Collector and specimen no.	Material state	Location	Herbarium
Sect. *Lunata*	*D. calycinum*	S.H. Yen T0957	Fresh	Botanical garden in Hung Kong	SYSU
	D. calycinum	L.C. Shih T1224	Fresh	Hung Kong	SYSU
	D. majus	S.H. Yen T1195	Fresh	Yunnan, China	SYSU
	D. majus	Y.M. Ho T1189	Fresh	Mt Da-wei, Bing-bian, Yunnan, China	SYSU
	D. majus	T. Sørensen et al. 3090	Dried	Chiengmai, Doi Sutep, Thailand	L
Sect. *Daphniphyllum*					
Subsect. *Staminodia*	*D. longeracemosum*	M.S. Tang & Y.M. Ho T1165	Fresh	Mt Da-wei, Bing-bian, Yunnan, China	SYSU
	D. longeracemosum	M.S. Tang T1179	Fresh	Fa-dou, Xi-chou, Yunnan, China	SYSU
	D. macropodum	M.S. Tang et al. T1202	Fresh	Tsukuba Botanical Garden, Japan	SYSU
	D. macropodum	M.S. Tang T1246	Fresh	Xiang-yang, Taidong, Taiwan	SYSU
	D. macropodum	M.S. Tang et al. T1259	Fresh	Wan-rong Forest Road, Hualien, Taiwan	SYSU
	D. macropodum	M.S. Tang T1270	Fresh	Mt Lan-qian, Ilan, Taiwan	SYSU
Subsect. *Daphniphyllum*					
Ser. *Daphniphyllum*	*D. borneense*	P. van Royen 7867	Dried	Mt Kinabalu, Sabah, Malaysia	L
	D. borneense	J.M.B. Smith 476	Dried	Mt Kinabalu, Sabah, Malaysia	L
	D. oldhamii	M.S. Tang T0698	Fresh	Da-zhi, Taipei, Taiwan	SYSU
	D. oldhamii	M.S. Tang T1136	Fresh	Mt Xian, Miaoli, Taiwan	SYSU
	D. oldhamii	M.S. Tang et al. T1244	Fresh	Mt Wang-zi, Kaohsiung, Taiwan	SYSU
	D. teijsmannii	L.C. Shih T1193	Fresh	Okinawa, Japan	SYSU
	D. teijsmannii	M.S. Tang et al. T1207	Fresh	Tsukuba Botanical Garden, Japan	SYSU
Ser. *Unicalycifera*	*D. buchananiifolium*	M.S. Tang T0917	Dried	Baguio, Luzon, the Philippines	SYSU
	D. buchananiifolium	M.S. Tang T0920	Dried	Baguio, Luzon, the Philippines	SYSU
Ser. *Longicalycifera*	*D. gracile*	M.J Wu et al. LAE 88822	Dried	Keglsugl, Papua New Guinea	LAE

Table 2 Comparison of leaf anatomical characters of nine species of *Daphniphyllum* observed from paraffin transverse sections (T.S.) and leaf clearings. Data between parentheses occur occasionally.

Classification	Species	Shape of epidermal cell (T.S.)		Shape of palisade cell (T.S.)	Layers of		Epidermal cell on adaxial surface			Stomata complex		Epidermal cell on abaxial surface	
		Adaxial	Abaxial		Palisade cell	Sponge cell	Shape	Anticlinal cell wall	Hypodermis	Type	Mean ± SE* length (μm)	Shape	Anticlinal cell wall
Sect. *Lunata*	*D. calycinum*	Oblong	Oblong	Conical to round	1	7~13	Irregular	Undulate	0	Hemiparacytic, brachyparacytic	20.2 ± 0.26	Irregular	Undulate
Sect. *Lunata*	*D. majus*	Oblong	Dome-shape	Conical to round	1	7~10	Irregular	Undulate	0	Hemiparacytic, brachyparacytic	24.0 ± 0.34	Irregular (polygonal)	Undulate (straight, curvy)
Sect. *Daphniphyllum* Subsect. *Staminodia*	*D. longeracemosum*	Oblong	Oblong	Conical	1	6~7	Polygonal	Straight to curvy	0	Brachyparacytic	22.2 ± 0.27	Polygonal, elongate	Straight, curvy
Subsect. *Staminodia*	*D. macropodum*	Oblong	Oblong	Conical to round	1~3	8~12	Polygonal	Straight to curvy	0	Brachyparacytic	26.9 ± 0.37	Polygonal, elongate	Straight, curvy
Subsect. *Daphniphyllum* Ser. *Daphniphyllum*	*D. borneense*	Square	Oblong	Columnar	2~3	9~11	Polygonal	Straight to curvy	0	Anomocytic, brachyparacytic	24.0 ± 0.46	Polygonal, elongate	Straight, curvy
Ser. *Daphniphyllum*	*D. oldhamii*	Oblong	Dome-shape	Columnar	1~3	10~13	Irregular	Undulate to curvy	0	Brachyparacytic	23.3 ± 0.36	Polygonal (irregular)	Curvy (undulate)
Ser. *Daphniphyllum*	*D. teijsmannii*	Oblong	Dome-shape	Columnar	1~3	6~9	Polygonal	Curvy	0	Brachyparacytic	23.1 ± 0.28	Isodiametric, elongate	Curvy
Ser. *Unicalycifera*	*D. buchananiifolium*	Square	Oblong	Columnar	2	9~12	Polygonal	Straight	1	Laterocytic, brachyparacytic	21.4 ± 0.58	Polygonal	Curvy
Ser. *Longicalycifera*	*D. gracile*	Square	Dome-shape	Columnar	1~3	8~10	Polygonal	Straight	1	Laterocytic, brachyparacytic	25.3 ± 0.44	Polygonal, elongate	Straight, curvy

* Values are means ± standard error.

Table 3 The typical leaf morphological characters for sections, subsections and series of *Daphniphyllum* observed in this study.

Taxon	Typical character
Sect. *Lunata*	Hemiparacytic stomata Irregular epidermal cells in shape on both surfaces Undulate anticlinal cell walls on both surfaces
Sect. *Daphniphyllum*	
Subsect. *Staminodia*	Conical to round palisade cells
Subsect. *Daphniphyllum*	Columnar palisade cells
Ser. *Daphniphyllum*	No hypodermis
Ser. *Longicalycifera* & *Unicalycifera*	Laterocytic stomata and 1-layered hypodermis

Epidermal cells

The adaxial epidermal cells show in transverse section two types of cellular shapes, square or oblong (Table 2). Square adaxial epidermal cells occur in *D. buchananiifolium* (Fig. 2c), *D. borneense* (Fig. 2g) and *D. gracile* of subsect. *Daphniphyllum*, and oblong epidermal cells appear in all the other species of both sect. *Daphniphyllum* and sect. *Lunata*.

The anticlinal walls on both surfaces of the epidermal cells of *Daphniphyllum* are straight, curved or undulate (Fig. 3). The type of anticlinal cell walls is constant on the species level, but varies between the species (Table 2). The two species of sect. *Lunata* show undulate anticlinal walls on both leaf surfaces (Fig. 3a–c). The anticlinal cell walls on both surfaces are straight, straight to curved or curved in all studied species of sect. *Daphniphyllum* except somewhat undulate in *D. oldhamii* (Fig. 3l).

The epidermal cells are polygonal, irregular, elongate and isodiametric in shape on both surfaces (Fig. 3, Table 2). Three species, *D. calycinum, D. majus* (both sect. *Lunata*) (Fig. 3c) and *D. oldhamii* (sect. *Daphniphyllum*) (Fig. 3l), have irregular epidermal cells on the adaxial side only, while the other species of sect. *Daphniphyllum* have polygonal adaxial epidermis (Fig. 3e, f, i, Table 2). Four epidermal shapes could be distinguished abaxially; seven species always show two shapes and only two species have a single type. The isodiametric shape is found only in leaves of *D. teijsmannii* (Fig. 3j) and restricted to the abaxial surface.

Hypodermis

A single layer of adaxial hypodermal cells (Table 2) is present in only two species, *D. buchananiifolium* (Fig. 2c) (subsect. *Daphniphyllum* ser. *Unicalycifera*) and *D. gracile* (Fig. 2f) (subsect. *Daphniphyllum* ser. *Longicalycifera*).

Stomata types

The stomata are restricted to the abaxial leaf surface only and randomly distributed. Four types of stomata are found, i.e. anomocytic, brachyparacytic, laterocytic and hemiparacytic (Table 2). The most common type is brachyparacytic, which is present in all nine taxa (Fig. 3a, b, d, g, h, j, k). The present study revealed three additional types of stomata in five species. The laterocytic type is present in *D. gracile* (ser. *Longicalycifera*) (Fig. 3g) and *D. buchananiifolium* (ser. *Unicalycifera*) (Fig. 3h); the hemiparacytic type is found in *D. calycinum* and *D. majus* (Fig. 3b) (sect. *Lunata*) and the anomocytic type in *D. borneense* (sect. *Daphniphyllum*).

The mean length of the guard cells varies between 20.2–26.9 μm (Table 2). *Daphniphyllum macropodum* has the longest guard cells and *D. calycinum* has the shortest ones.

We summarized the typical leaf morphological characters for different taxa in Table 3. First, hemiparacytic stomata, irregular epidermal cells and undulate anticlinal cells on two sides

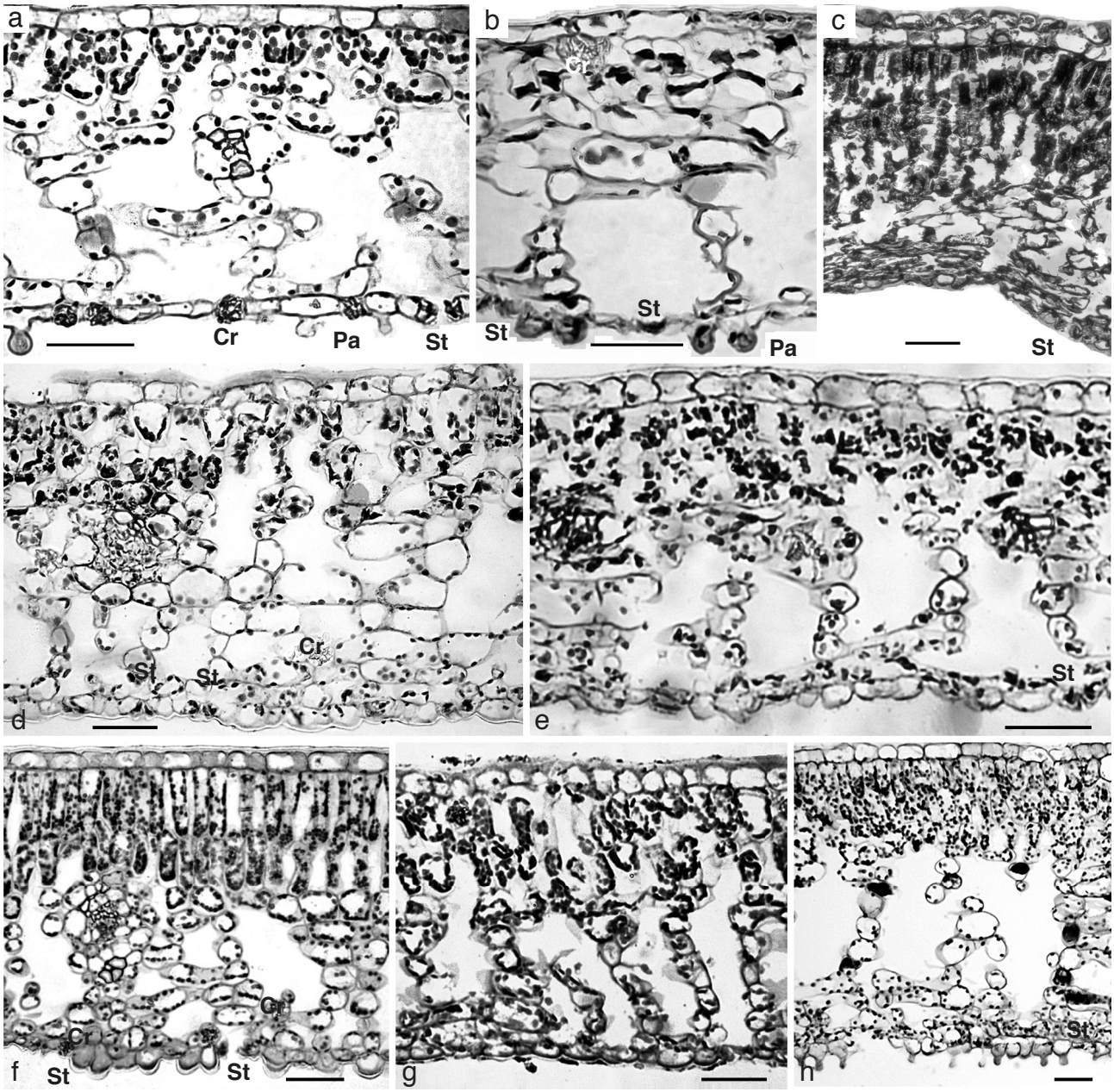

Fig. 2 Light microscopy photographs of transverse leaf sections of *Daphniphyllum* species. a, b. Sect. *Lunata*; c, f–j. subsect. *Daphniphyllum*; d, e. subsect. *Staminodia*. — a. *D. calycinum*; b. *D. majus*; c. *D. buchananiifolium*; d. *D. macropodum*; e. *D. longeracemosum*; f. *D. teijsmannii*; g. *D. borneense*; h. *D. oldhamii*. — Abbreviations: Cr = crystal; Pa = Papillae; St = stomata complex. — Scale bars = 50 µm.

are characteristic for sect. *Lunata*. Secondly, the outstanding character typical for subsect. *Staminodia* and *Daphniphyllum* of sect. *Daphniphyllum* is the shape of the palisade cells (conical to round vs columnar). Finally, we also can distinguish ser. *Longicalycifera* and *Unicalycifera* from subsect. *Daphniphyllum* based on laterocytic stomata and a 1-layered hypodermis, but there is no other available character to further differentiate both series. The characters mentioned above may serve as remarkable taxonomic characteristics for the genus *Daphniphyllum*.

DISCUSSION

Huang (1965) reported that the genus *Daphniphyllum* shows two distinct types of mesophyll tissue, i.e. well differentiated palisade and spongy layers and poorly differentiated palisade and spongy layers. This is confirmed by our study. Huang (1965) also indicated that *D. angustifolium* (sect. *Daphniphyllum* subsect. *Staminodia*) possesses a well-differentiated mesophyll and an adaxial hypodermis. However, the specimens of the two investigated species (*D. macropodum* and *D. longeracemosum*) of the same subsection did not reveal Huang's characters at all. Moreover, these features "well differentiated mesophyll tissue and adaxial hypodermis" as Huang found for *D. angustifolium* (subsect. *Staminodia*) were only found in two of the five species of subsect. *Daphniphyllum* in this study. Based on these results, we assume that a relatively close relationship may occur between *D. angustifolium* and subsect. *Daphniphyllum*.

Four types of stomata are found, i.e. brachyparacytic, hemiparacytic, laterocytic and anomocytic; the latter two types are first reported here. These distinctive stomatal types can be important characters for an infrageneric classification. Paracytic stomata were the only type reported for *Daphniphyllum* so far (Huang 1965, Metcalfe & Chalk 1988, Zhang & Lu 1989). However, the brachyparacytic type may just be a more specific term than the one used in any of the earlier articles (Huang 1965 in Fig. 3, Zhang & Lu 1989 in Plate 1). Furthermore, laterocytic stomata are first reported here, but we notice that they were already visible for *D. gracile* in Huang (1965: f. 3). Anomocytic stomata

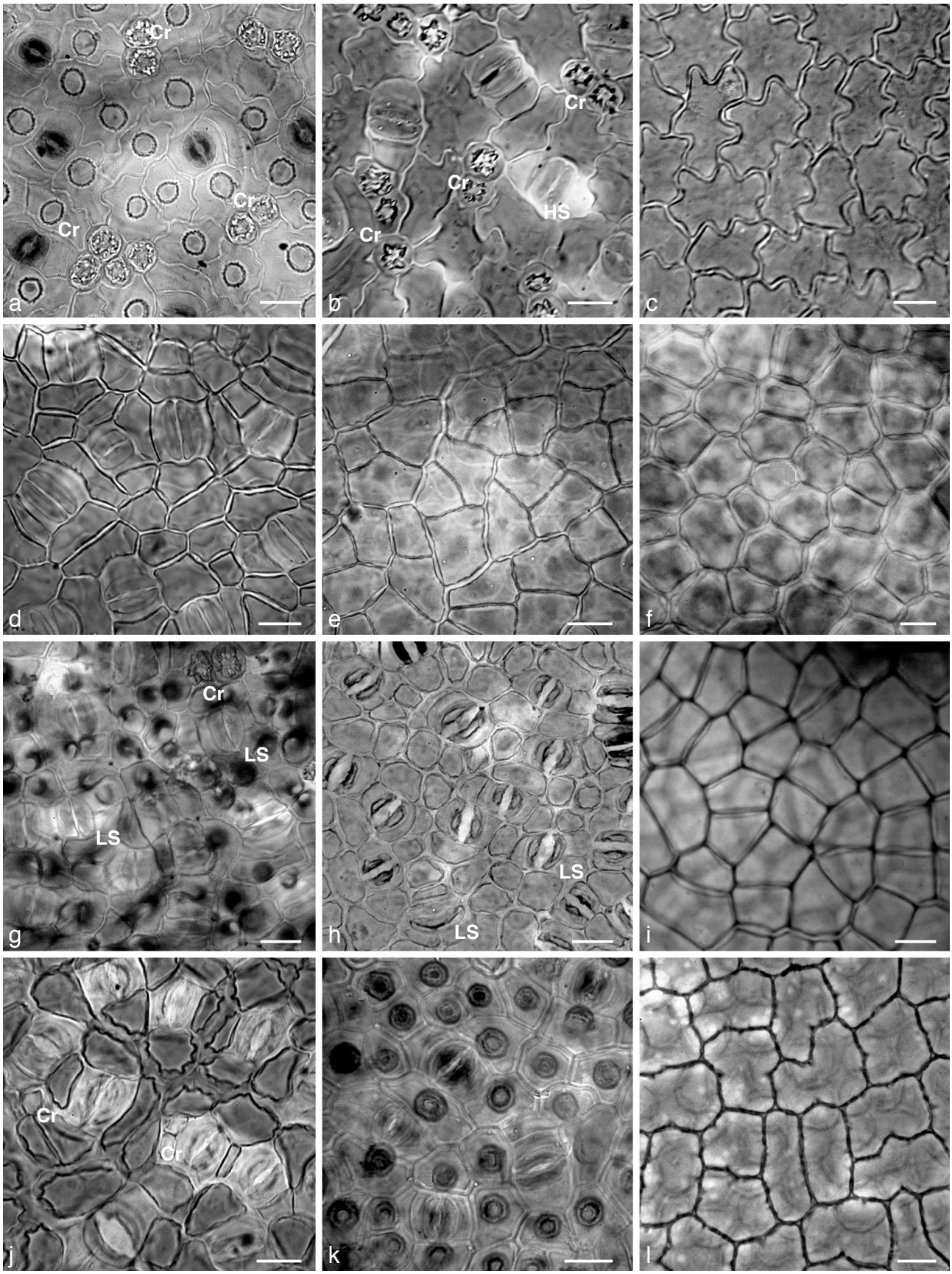

Fig. 3 Light microscopy photographs of the leaf epidermis of *Daphniphyllum* species. a, b, d, g, h, j, k. Abaxial view; c, e, f, i, l. adaxial view. a. *D. calycinum*; b, c. *D. majus*; d, e. *D. macropodum*; f. *D. borneense*; g. *D. gracile*; h, i. *D. buchananiifolium*; j. *D. teijsmannii*; k, l. *D. oldhamii*. — Abbreviations: Cr = crystal; HS = hemiparacytic stomata; LS = laterocytic stomata. — Scale bars = 20 µm.

only occur in *D. borneense*. The hemiparacytic stomatal type exclusively occurs in sect. *Lunata*, while the laterocytic stomata only appear in ser. *Longicalycifera* and *Unicalycifera* of subsect. *Daphniphyllum*.

Huang (1996, 1997) treated *D. gracile* (ser. *Longicalycifera*) and *D. buchananiifolium* (ser. *Unicalycifera*) in different series. However, the anatomical characters like hypodermis, straight anticlinal adaxial cell walls and laterocytic stomata may point to a closer relationship between these species. The various ranges of stomatal types may be an aid to recognize the different infrageneric taxa within the *Daphniphyllaceae*.

Within the nine studied species, *D. oldhamii* and *D. teijsmannii* are similar in morphological character. Huang (1966) distinguished them by papillose/epapillose on the abaxial surface of leaves. However, Huang (1965) and Wang (1981) mentioned that the character of papillae is unstable in *D. oldhamii*, so that identification of the two species is difficult. Our results show distinguishing differences in the epidermis. *Daphniphyllum oldhamii* has undulate and irregular adaxial epidermal cells, while *D. teijsmannii* not only shows straight and curved anticlinal cells on the adaxial surface but it also has isodiametric abaxial epidermal cells. Other studied species of the series can also be distinguished by two characters, shape of epidermal and size of guard cells (Table 2). For example, *D. calycinum* and *D. majus* of sect. *Lunata* can be distinguished by the characters oblong abaxial epidermis/smaller (20.2 µm) guard cells vs dome-shape abaxial epidermis/bigger (24.0 µm) guard cells. Due to the overlap of anatomical characters among the species of subsect. *Staminodia*, and between the species of ser. *Longicalycifera* and *Unicalycifera*, the size of guard cells is the only one character to support the classification.

The undulate anticlinal cell walls of both epidermal layers, the irregular epidermal cells of upper and lower surfaces, and the hemiparacytic stomata are typical characters of sect. *Lunata*. Anatomically, these three characters may well support the theory that sect. *Lunata* is likely to be a natural group. However, the leaf anatomical characters within sect. *Daphniphyllum* are highly divergent, which may imply that the current infrasectional classification is artificial. Furthermore, Huang (1965) pointed out that the two sections *Staminodia* (currently subsect. *Staminodia* of sect. *Daphniphyllum*) and *Calycifera* (currently subsect. *Daphniphyllum*) are artificial sections. The limited samples of sect. *Daphniphyllum* in this study may be inadequate to draw firm conclusions for classification of sect. *Daphniphyllum.* Therefore, more comprehensive studies on sect. *Daphniphyllum* are still warranted.

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