Taiwania, **48**(4): 213-223, 2003

Comparative Study on the Stinging Trichomes and Some Related Epidermal Structures in the Leaves of *Dendrocnide meyeniana*, *Girardinia diversifolia*, and *Urtica thunbergiana*

Han-Yi Fu[(1)], Shiang-Jiuun Chen[(1)], and Ling-Long Kuo-Huang[(1,2)]

(Manuscript received 8 September, 2003; accepted 23 October, 2003)

ABSTRACT: In this study, the morphology and distribution of the stinging trichomes and the related epidermal structures in the mature leaves of *Dendrocnide meyeniana*, *Girardinia diversifolia*, and *Urtica thunbergiana* are compared. On the adaxial and abaxial leaf surfaces, stinging trichomes, glandular, and non-glandular (hispid and pustulate) were observed. Among these studied species, the stinging trichome of *Dendrocnide meyeniana* is the shortest, but the density on the adaxial surface is the highest. In *Girardinia diversifolia*, the stinging trichomes are the longest, but the density is the lowest. The major elements of stinging cells of all the studied plants are silicon and calcium. In *Dendrocnide meyeniana*, the average silicon/calcium ratio is the highest, while the lowest silicon/calcium ratio was found in the stinging cells located on the veins of abaxial surface in *Urtica thunbergiana*. In *Girardinia diversifolia*, the amount and surrounding area of pedestal cells are the highest while in *Dendrocnide meyeniana*, however, are the lowest. On the leaf surface of *Urtica thunbergiana*, not any hydathode was observed, while pearl glands were only found in the leaves of *Dendrocnide meyeniana*. Calcium carbonate and oxalate depositions were found in all the studied stinging species.

KEY WORDS: Stinging trichome, Pedestal cell, Hydathode, Pearl gland, Calcium deposition, *Dendrocnide meyeniana, Girardinia diversifolia, Urtica thunbergiana*.

INTRODUCTION

In the most species of Urticaceae, various epidermal structures, like different types of trichomes, calcium depositions and hydathodes, are distributed on leaves. The trichomes are generally grouped into glandular, non-glandular and stinging trichomes. Since the first published description by Hooke in 1665, the stinging trichomes have been studied by many investigators (Thurston and Lersten, 1969; Pollard and Briggs, 1984; Lin *et al*., 1991; Corsi, 1992; Fodor and Cseh, 1993; Tuberville *et al.*, 1996). The stinging trichomes of *Urtica* consist of a stinging cell with surrounding pedestal cells. When a touch with the human skins, the toxin in the stinging trichomes is released to human and gives pain, wheal, or stinging sensation, and the sensation can be lasted for several hours (Oliver *et al.*, 1991; Taskila *et al.*, 2000). In addition to defending to animals, the function of the stinging trichomes is also regarded as secretion of metabolites (Corsi, 1999).

Besides in the Urticaceae, the stinging trichomes are also known to occur in the families of Euphorbiaceae, Loasaceae, and Hydrophyllaceae (Thurston and Lersten, 1969). However, in Taiwan, the stinging trichomes were only reported in the species of the tribe Urticeae in Urticaceae (Lin, 1991; Yang *et al*., 1996; Su, 2000). In a preliminary investigation of these

1. Department of Life Science, College of Life Science, National Taiwan University, Taipei 106, Taiwan.
2. Corresponding author. Email: linglong@ntu.edu.tw. Fax: 00886-2-23918940.

stinging plants, we found that the types, morphology and distribution of trichomes are different among species and may have contribution in the plant systematics and ecology (Ehleringer and Cook, 1987; Hannan, 1988; Webster, 1996; Tae *et al*., 1997). This study was undertaken to compare the stinging trichomes and some related epidermal structures in the leaves of three most common stinging plants in Taiwan: *Dendrocnide meyeniana*, *Girardinia diversifolia*, and *Urtica thunbergiana*.

MATERIALS AND METHODS

Plants of *Dendrocnide meyeniana*, *Girardinia diversifolia*, and *Urtica thunbergiana* were collected (Table 1) and planted in the green house of Department of Life Science, National Taiwan University. For paraffin-sectioning, the leaf and petiole segments were fixed in formalin-propranol-glycerol-alocohol (FPGA), dehydrated in tertiary butyl alcohol series, embedded in paraffin, sectioned on a rotary microtome (in 12-16 μm thick), and stained in Safranin O and fast-green. The observation and micrographs were made with a Leica Diaplan Microscope. Clearing technique (Kuo-Huang *et al*., 2002) was used specifically to locate the calcium oxalate crystals. The materials for scanning electron microscopy (SEM) were fixed in 2.5% glutaraldehyde in 0.1 M phosphate buffer followed by 1% OsO_4, dehydrated in ethanol-acetone series, dried with a Hitachi Critical Point Dryer (HCP-1), coated with an IB-2 ion coater (Dawes, 1979), and examined with the Hitachi S-800 SEM. For energy dispersive X-ray microanalysis (EDX), the samples were fixed in FPGA, dehydrated in ethanol-acetone series, dried with HCP-1, carbon-coated with an IB-2 ion coater, and examined with the Kevex Level Four EDS and Hitachi S-2400 SEM.

Table 1. Taxa used in this study.

Taxon	Collection date	Collection site
Dendrocnide meyeniana (Walp.) Chew	2002. 7.	Heng-chun, Ping-tung County
Girardinia diversifolia (Link) Friis	2002. 9.	Dung-shih, Tai-chung County
Urtica thunbergiana Sieb. & Zucc.	2002. 9.	Fu-shan, I-lan County

RESULTS

In the mature leaves of *Dendrocnide meyeniana*, *Girardinia diversifolia*, and *Urtica thunbergiana*, different kinds of trichomes, hydathodes, and calcium depositions were observed. The types and distribution of these epidermal structures are summarized in Tables 2 and 3, and the detail characteristics are described below.

Table 2. The epidermal structures on mature leaves of the studied stinging plants of Urticaceae.

Taxon	Trichome		Hydathode	Calcium deposition		Pearl gland
	adaxial	abaxial		cystolith	calcium oxalate	
Dendrocnide meyeniana	ST, GT, HT	ST, GT, HT	+	+	Raphides	+
Girardinia diversifolia	ST, GT, PT	ST, GT, PT	+	+	Druses	-
Urtica thunbergiana	ST, GT, HT	ST, GT, HT, PT	-	+	Druses	-

ST = stinging trichome; GT = glandular trichome; HT = hispid trichome; PT = pustulate trichome.

Glandular trichomes and non-glandular trichomes

Both the glandular and non-glandular tirchomes were found in the adaxial and abaxial epidermis of all the studied species (Table 2; Figs. 1A-G). The non-glandular trichomes are unicellular and cone shape. Based on the surface structure, they are divided to hispid and pustulate trichomes. The pustulate trichomes have protuberance on the outer cell wall and generally longer than the hispid trichomes (Figs. 1C-E and G). The pustulate trichomes were found in both the adaxial and abaxial epidermis of *Girardinia diversifolia*, but only on the leaf veins of the abaxial surface of *Urtica thunbergiana* (Table 2; Fig. 1G). Nevertheless, the hispid trichomes were found in both the adaxial and abaxial epidermis of *Dendrocnide meyeniana* and *Urtica thunbergiana*.

In *Dendrocnide meyeniana* and *Urtica thunbergiana* the glandular trichomes are sporadically distributed on both leaf surfaces and generally are four-head-celled (Figs. 1C and E). However, in *Girardinia diversifolia* the glandular trichomes were usually found as two-head-celled. Except occurring on the leaf surface, they were also found on the base of the stinging trichomes (Figs. 2C and D). The hispid trichomes in *D. meyeniana* are distributed mostly on or near the leaf veins (Figs. 1B and C). Compared to *D. meyeniana*, the hispid trichomes in *U. thunbergiana* have obvious swelling base (Fig. 1F). In *G. diversifolia*, the pustulate trichomes have swelling bases (Figs. 1D and E). On the adaxial leaf surface, their orientation are mostly pointed to the leaf apex.

Table 3. Properties of the stinging trichomes in the studied species.

Taxon	Distribution		Length [a] (mm)	Number per leaf surface	Density on the adaxial surface [b] (No. / cm^2)
	adaxial	abaxial			
Dendrocnide meyeniana	both intercostal and veins		0.37±0.07	>1000	47.47±9.32
Girardinia diversifolia	intercostal	1° and 2° veins	5.62±0.45	<100	0.93±1.72
Urtica thunbergiana	intercostal	1° and 2° veins	2.65±0.21	200-300	3.20±2.66

Sampling numbers: a, n = 10; b, n = 30.

Stinging trichomes

The stinging trichomes were found in both the adaxial and abaxial leaf surfaces of all the studied species (Tables 2, 3). In *Dendrocnide meyeniana*, they sporadically occur in both the intercostal and vein areas. While in *Girardinia diversifolia* and *Urtica thunbergiana*, the stinging trichomes are located on the adaxial intercostal areas as well as on the abaxial areas of the first and second leaf minor veins.

The diameters of the stinging cells are decreased acropetally. The tips of stinging cells are globular (Figs. 2A, C and H) and the "neck" areas are fragile when touched. In *Girardinia diversifolia* and *Urtica thunbergiana* (Fig. 2I), cyclosis of cytoplasm was observed in the middle and basal parts of the stinging cells, but could not be found in the upper part.

Among these studied stinging plants, the morphology of the stinging cells and the relative locations of surrounding pedestal cells are different. The stinging trichome of *Dendrocnide meyeniana* is the shortest, but the density of the stinging trichomes on the adaxial surface is the highest (Table 3). The number of stinging trichomes per leaf is over 1000. While in *Girardinia diversifolia*, the stinging trichomes are the longest. But the density of the stinging trichomes is the lowest. The number of stinging trichomes per leaf is fewer than 100.

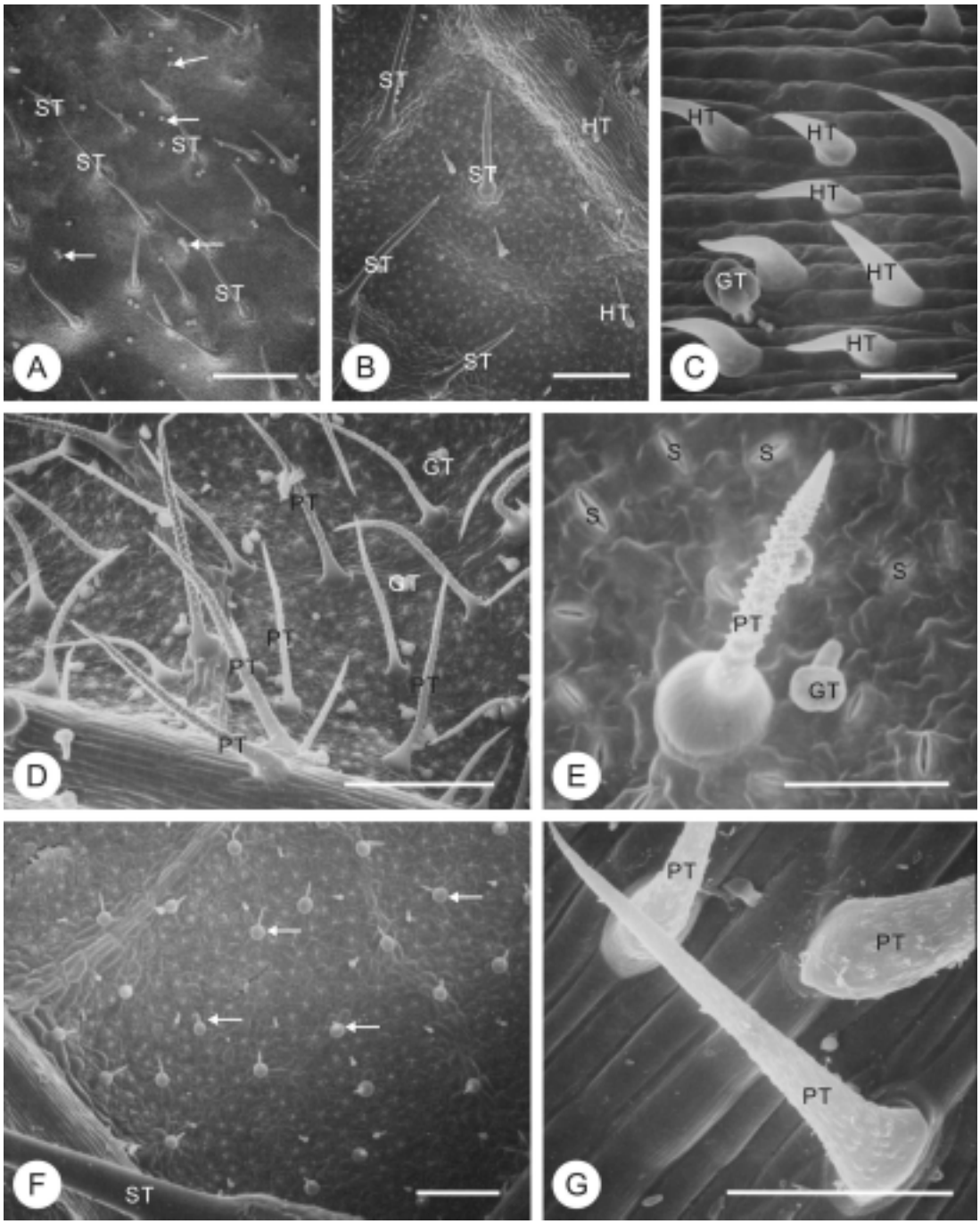

Fig. 1. A-G. SEM photographs. A-C, *Dendrocnide meyeniana*. A, Adaxial leaf surface showing the stinging trichomes and glandular trichomes (arrows) dispersed distributed on the surface. Bar = 500 μm. B, Abaxial leaf surface showing the stinging trichomes dispersed distributed in the intercostal areas or on the veins while the hispid trichomes distributed mostly on the veins. Bar = 200 μm. C, Abaxial surface showing many hispid trichomes and fewer glandular trichomes distributed on the mid vein. Bar = 50 μm. D and E, *Girardinia diversifolia*. D, SEM photograph of abaxial surface showing the distribution of pustulate trichomes and glandular trichome. Bar = 200 μm. E, Abaxial surface showing the pustulate and glandular trichomes. Bar = 50 μm. F and G, *Urtica thunbergiana*. F, Abaxial leaf surface showing many hispid trichomes (arrows) with bulbous base distributed mostly in the intercostal area. Bar = 200 μm. G, Abaxial surface showing the fine structure of pustulate trichomes on the vein. Bar = 50 μm. (GT = glandular trichome; HT = hispid trichome; PT = pustulate trichome; S = stomata; ST = stinging trichome).

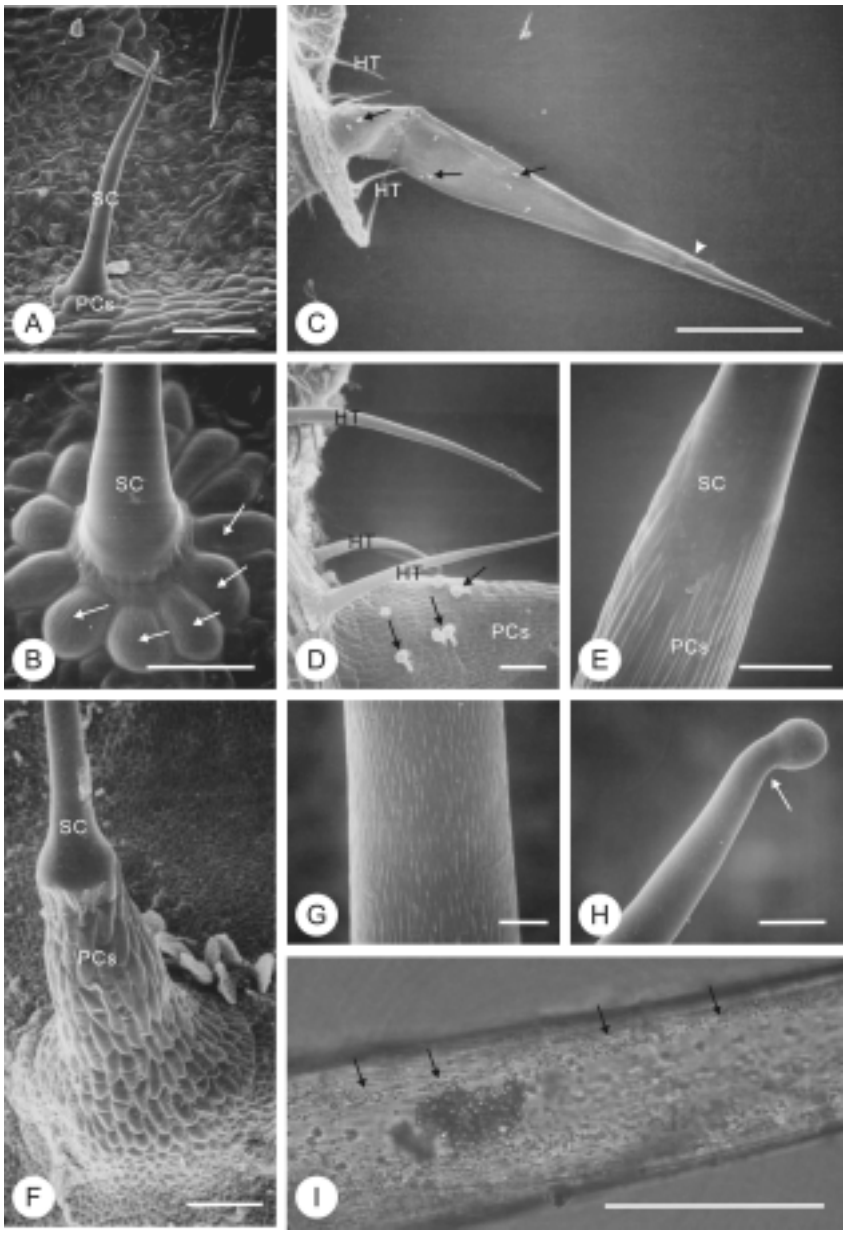

Fig. 2. A-F, SEM photographs. I, LM photograph. A and B, *Dendrocnide meyeniana*. A, Abaxial leaf surface showing a stinging trichome on the vein. Numberous stomata occurred mostly in the intercostal area. Bar = 100 μm. B, Enlargement of (A) showing the base of the stinging trichome. The stinging trichome consists of a large stinging cell with about 10-12 pedestal cells (arrows) surrounding the base. Bar = 50 μm. C-E, *Girardinia diversifolia*. C, A stinging trichome on the vein of adaxial surface. Some glandular trichomes (arrows) can be found on the lower and middle surface of the stinging trichome. Many hispid trichomes are near the stinging trichome. Bar = 1000 μm. D, Enlargement of (C) on the lower part of the stinging trichome showing the pedestal cells surrounding large part of the stinging cell and some glandular trichomes (arrows) occurring on the pedestal cells. The hispid trichomes locate near the stinging trichome. Bar = 100 μm. E, Enlargement of (C) arrowhead showing irregular end of surrounding pedestal cells. Bar = 100 μm. F-I, *Urtica thunbergiana*. F, The lower part of the stinging trichome showing the pedestal cells emergent from epidermis and surrounding the base of the stinging cell. Bar = 200 μm. G, The ridges on the stinging cell wall. Bar = 20 μm. H, The top region of the stinging cell showing the spherical structure on the upmost part and below which the abruptly narrowest "neck" (arrow). Bar = 20 μm. I, Cyclosis of some unknown particles (arrows) in the cytoplasm of the stinging cell in *Urtica thunbergiana*. Bar = 200 μm. (HT = hispid trichome; PCs = pedestal cells; SC = stinging cell).

The stinging trichome of *Dendrocnide meyeniana* has only 10-20 pedestal cells (Figs. 2A and B). The basal parts of the stinging cells are embedded in the epidermis and the surrounding pedestal cells are located on the epidermis. While in *Girardinia diversifolia*, the pedestal cells are enclosed over half surface of the stinging cells. The layers of surrounding pedestal cells are decreased from multilayered to single-layered acropetally and, in general, have irregular ending on the top of stinging cells (Fig. 2E). In *Urtica thunbergiana*, the pedestal cells are enclosed only the basal parts of the stinging cells (Fig. 2 F).

In *Girardinia diversifolia* and *Urtica thunbergiana*, the adaxial surface of leaf where the stinging trichomes located is obviously bulged, and the basal parts of the stinging trichomes are also raised from the leaf surface (Fig. 2F). There are tiny ridges on the outer walls of stinging cells of *G. diversifolia* and *U. thunbergiana* (Fig. 2G), but not in *Dendrocnide meyeniana* (Fig. 2B).

The results of EDX microanalysis tests (Table 4) showed that the major elements of stinging cells of all the studied plants are silicon and calcium. In *Dendrocnide meyeniana*, the average silicon/calcium ratio is the highest. The lowest silicon/calcium ratio was found in the stinging cells located on the veins of abaxial surface in *Urtica thunbergiana*.

Table 4. Si/Ca ratio of atomic number by EDX on the base, middle, and top of the stinging trichomes.

Si / Ca Ratio	*Dendrocnide meyeniana*	*Girardinia diversifolia*	*Urtica thunbergiana**	*Urtica thunbergiana***
Top	24.64	2.01	3.51	1.60
Middle	8.31	4.06	3.20	0.47
Base	11.18	3.44	6.02	1.90
Average	14.70	3.17	4.24	1.32

* intercostal stinging trichome; ** stinging trichome on the vein of the abaxial surface.

Hydathodes and Pearl glands

Hydathodes were found in the adaxial epidermis of the mature leaves in *Dendrocnide meyeniana* and *Girardinia diversifolia* (Table 2; Fig. 3A and B). In *D. meyeniana*, the hydathodes are randomly distributed. However in *G. diversifolia*, they are arranged near the stinging trichomes and the pustulate trichomes (Figs. 3A and B). It is interesting to note that during the leaf growth of *D. meyeniana*, many pearl glands could be observed (Fig. 3C). They are distributed along the petioles and the leaf veins, especially on the basal areas of the leaf. Pearl glands are multicellular and with a multicellular glandular trichome on the top.

Calcium depositions

Both calcium carbonate and calcium oxalate depositions were observed in the studied species (Table 2). The cystoliths mainly consist of calcium carbonate and were found in the lithocysts occurred in the adaxial epidermis (Fig. 3D). In *Dendrocnide meyeniana* the calcium oxalate crystals are raphides and mostly dispersedly distributed in the intercostal mesophyll (Fig. 3E). However, in *Girardinia diversifolia* and *Urtica thunbergiana*, they are druses. In *G. diversifolia*, many calcium crystals are densely distributed along the veins or sporadically occurred in the intercostal mesophyll (Figs. 3F and G). In *U. thunbergiana*, calcium crystals are located beside the vascular bundle of the vein (Fig. 3H).

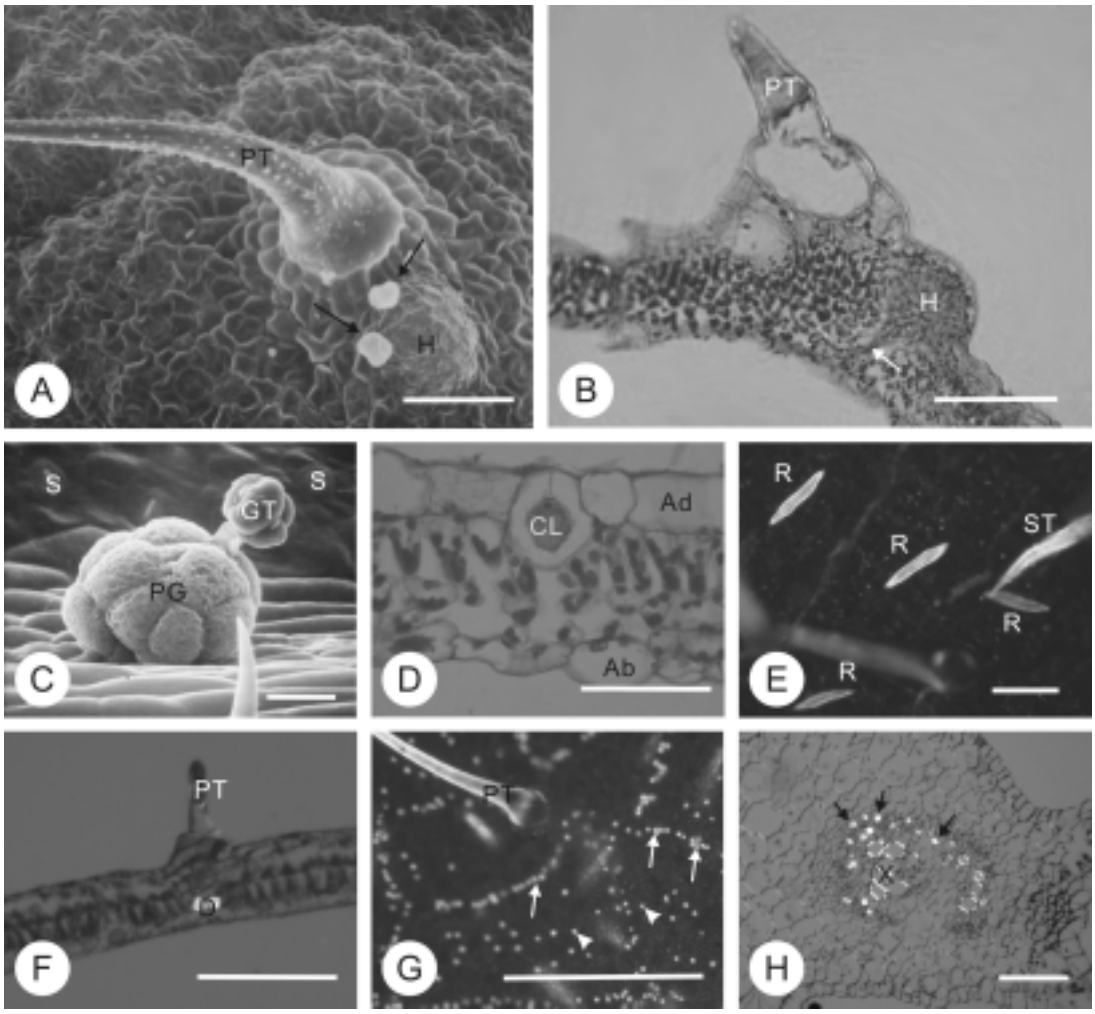

Fig. 3. A and B, *Girardinia diversifolia*. A, SEM photograph of a pustulate trichome on the adaxial leaf surface. Hydathode are located near the pustulate trichome and some glandular trichomes (arrows) are distributed near the hydathode. Bar = 100 µm. B, LM photograph of a transverse section of mature leaf showing the hydathode located on the adaxial leaf surface and with vascular bundle connected (arrow). Bar = 100 µm. C, SEM photograph showing the pearl gland occurred on the abaxial surface in *Dendrocnide meyeniana*. A glandular trichome is found on the top of pearl gland. Bar = 500 µm. D, LM photograph of a trasverse section of mature leaf of *Urtica thunbergiana* showing the cystolith occurring in the lithocyst of the adaxial epidermis. Bar = 50 µm. E-H, Partial polarized LM photographs. E, The cleared leaf of *Dendrocnide meyeniana* showing many raphid type of calcium oxalate crystals and the stinging trichome. Bar = 100 µm. F, Part of transverse section of mature leaf showing the druse type of calcium oxalate crystals in the mesophyll in *Girardinia diversifolia*. Bar = 100 µm. G, In the cleared mature leaf of *Girardinia diversifolia*, many calcium oxalate crystals distributed along the veins (arrows) or sporadically occurred in the mesophyll (arrowheads). Bar = 500 µm. H, Part of transverse section of mature leaf showing the druse type of calcium oxalate crystals (arrows) near the vascular bundle of the vein in *Urtica thunbergiana*. Bar = 100 µm. (Ab = abaxial epidermis; Ad = adaxial epidermis; CL = cystolith; D = druse; GT = glandular trichome; H= hydathode; PT = pustulate trichome; R = raphid; S = stomata; X = xylem).

DISCUSSION

As the stinging trichomes are diversely occurring in four unrelated families, Urticaceae, Euphorbiaceae, Loasaceae, and Hydrophyllaceae (Thurston and Lersten, 1969), it is believed

as a good example of convergent evolution. In Urticaceae, the stinging trichomes are not homologous (Thurston, 1974). Their structures and the toxic extracts may be different between species and genera (MacFarlane, 1963). Besides, the location of surrounding pedestal cells observed in these three studied species is similar with the previous study (Thurston and Lersten 1969) and that shows it may be a comparable characteristic of these three genera. Although in *Dendrocnide kotoensis*, there are no poisonous stinging trichomes (Yang *et al.*, 1996).

The functions of epidermis are water regulation, protection against sunlight and defense to other organisms (Mauseth, 1988). The occurrences of trichomes are common in Urticaceae, and the different trichomes may contribute some function described by Mauseth (1988). Besides, the high density of trichomes may disturb the movement of invertebrates. The density of the stinging trichomes was increased when the plants were grown on the region where the leaves were easily eaten or harmed by herbivores. So it is regarded as the strategy of defense (Pollard, 1986; Tuberville *et al*., 1996). During the experimental period of this study, the density of stinging trichomes in *Girardinia diversifolila* was decreased during the leaf growth. However, no obvious scars eaten by herbivores were observed.

The ecological conditions of the habitats of the three studied stinging plants are varied. Trees of *Dendrocnide meyeniana* are naturally distributed under full sunlight in low altitude, while herbs of *Girardinia diversifolia* and *Urtica thunbergiana* are mostly growing under shade and in somewhat wet habitat.

Although stinging trichomes in the studied plants are diverse in structure, there are still some identical features. The globular tips of the stinging trichomes may associated with penetrating human skins and give pain sensation, and the fragile top of the stinging trichomes may leave the tips in the skins. The cyclosis of cytoplasm in stinging trichomes was reported in *Urtica dioica* by Wiesner (1906). Perhaps due to the small size of the stinging cells in *Dendrocnide meyeniana*, no cyclosis was observed. In *Girardinia diversifolia* and *Urtica thunbergiana*, the cyclosis occurs from the basal to the middle areas of the stinging cell, but in the upper area (about one fifth of the stinging cell), it abruptly slows down. Because the pain sensation occurs after the transient touching the stinging trichomes, it does not seem that the cytoplasmic streaming of the stinging cell was fast enough to release the toxic substance. So it may be a special mechanism on rapid release of toxin, or the globular tips of the stinging trichomes may contribute to the stinging properties.

The cell wall of stinging cell contains silicon and calcium, and silicon is the necessary factor to cause the stinging sensation (Fodor and Cseh, 1993). Haberlandt (1886) described that the silicon concentration basipetally decrease while the calcium increased in the same direction. But Thurston (1974) thought that the lower part of the stinging cells contains neither silicon nor calcium by X-ray microanalysis. In our results by EDX microanalysis, the cell walls of the stinging trichomes of these three studied species contain silicon and calcium overall. The silicon compound of the cell wall may be confirmed from the lightening of stinging cell by polarized-light microscopy (Fig. 3E). In *Dendrocnide meyeniana*, the average silicon / calcium ratio is highest (14.7) of the studied species. When the stinging trichomes of *Girardinia diversifolia* and *Urtica thunbergiana* were put in concentrated hydrochloric acid, the air bubbles occurred inside the top of the stinging cell. The bubbles were probably due the existence of calcium carbonate in cytoplasm which may lower the silicon / calcium ratios of these two species. From the EDX data of different parts in the same stinging cell, it does not seem that the silicon / calcium ratios are decreased basipetally. Further study is necessary to be undertaken to find the silicon and calcium distribution of the stinging cell.

The toxic stinging properties are regarded as one of the function of stinging trichomes. Besides, they may be involved in the elimination of unnecessary minerals and water. Corsi (1999) suggested that the primary function of stinging trichomes might be the regulation between the plant and the environment. Concerning the results of study on calcium, it seemed that the stinging trichomes might be associated with the calcium metabolism. In the leaves of the studied species, some calcium ions may be incorporated to the calcium oxalate crystals and the cystoliths or they may enter the stinging cell and be incorporated into the cell wall. In sum, the calcium metabolites are storied in many ways in the stinging plants.

The elimination of metabolites or water may be used by the secretion of hydathodes. The close neighbors of hydathodes with hispid or stinging trichomes in *Girardinia diversifolia* show that they might be with some functional associations. The occurrence of pearl glands in *Dendrocnide meyeniana* is also a possible way to secret salts or metabolites. The frequency of pearl glands may be associated with the environmental change. The pearl glands in *Urtica dioica* were present only after transfer to hot, humid greenhouse (Corsi, 1999). In our preliminary experiment of tissue culture of *Dendrocnide meyeniana*, a large amount of pearl glands occurred on the segments of petioles when incubated in MS medium with 0.3 ppm NAA + 3 ppm kinetin or 3 ppm NAA + 0.3 ppm kinetin. So it is suggested that the occurrence of pearl glands may be due to the increasing of environmental salt concentration.

It is very interesting to concern the convergent evolution of stinging trichomes among the diverse plants. The stinging effects are more than one possible mechanism in different families (Thurston, 1976). Although the toxins of stinging cells in *Urtica* spp. were regarded as acetylcholine, histamine and serotonin, other possible toxins were also reported (Czarnetzki *et al.*, 1990, Antonopoulou *et al*., 1996, Taskila *et al*., 2000). The research of the mechanisms of stinging properties of different species still has much space to proceed. In the three stinging plants belong to different genera in Urticaceae, our observation on the leaf morphology indicates that there are some diversity and homology of the trichomes and other structures. The difference of density, size of stinging trichomes, distribution of pedestal cells and others have provided some information for systematics. However, the similarity of the structure of stinging trichomes, homology of glandular trichomes and calcium depositions indicate the functional relationships of the three species.

ACKNOWLEGEMENTS

We thank Feng-Yi Ma for providing the useful ideas and are also grateful for the technical support from Ching-Yen Lin and Chih-Yuan Tang in the Electron Microscope Center of National Taiwan University.

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咬人狗、蝎子草和咬人貓葉部燅毛與相關表皮構造的比較

傅瀚儀[1]、陳香君[1]、黃玲瓏[1,2]

(收稿日期：2003 年 9 月 8 日；接受日期：2003 年 10 月 23 日)

摘　　要

本研究比較咬人狗、蠍子草和咬人貓的燅毛與相關表皮構造形態與分佈上的異同。在葉部上下表皮中可以發現到燅毛、腺毛和非腺毛（硬狀毛茸與表面瘤狀毛茸）的存在。在研究中觀察到咬人狗的燅毛最短，但在上表皮的密度最高；蠍子草的燅毛最長，密度卻最低。燅毛細胞內含的主要元素為矽和鈣。咬人狗的平均矽/鈣比最高，而咬人貓下表皮葉脈上的燅毛細胞平均矽/鈣比最低。蓮座細胞的數量與覆蓋程度以蠍子草最多，咬人狗最少。咬人貓葉表並沒有發現泌水器，三者中只有咬人狗葉表上發現珍珠狀腺體存在。碳酸鈣與草酸鈣沈澱都可以在這三種植物葉子中找到。

關鍵詞：燅毛、蓮座細胞、泌水器、珍珠狀腺體、鈣沈澱物、咬人狗、蠍子草、咬人貓。

1.國立台灣大學生命科學院，生命科學系，台北市 106，台灣。
2.通信作者。Email: linglong@ntu.edu.tw. Fax: 00886-2-23918940.