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Genetics and Morphology Associated With the Flowering Pattern, Flowers, and Leaves of Capsicum Annuum L. And Capsicum Chinense Jacq.

Dai-mei Shuh
Louisiana State University and Agricultural & Mechanical College

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Genetics and morphology associated with the flowering pattern, flowers, and leaves of *Capsicum annuum* L. and *Capsicum chinense* Jacq.

Shuh, Dai-Mei, Ph.D.
The Louisiana State University and Agricultural and Mechanical Col., 1989
GENETICS AND MORPHOLOGY
ASSOCIATED WITH THE FLOWERING PATTERN, FLOWERS, AND LEAVES OF
Capsicum annuum L. AND Capsicum chinense Jacq.

A Dissertation

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Agricultural and Mechanical College
in Partial Fulfillment of the
Requirements for the Degree of
Doctor of Philosophy

In
The Department of Horticulture

By
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B.S., National Chung-Hsing University, 1976
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August 1989
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Abstract

The leaves and the flowers of *Capsicum annuum* L. and *Capsicum chinense* Jacq. were morphologically and genetically studied. *C. annuum* sets one flower at each node; *C. chinense* sets multiple (two or three) flowers at each node. 'Serrano Chili' (*C. annuum* L.) has an unique pubescent leaf type. The study on the interspecific hybridization between 'Serrano Chili' and No. 178 (*C. chinense* Jacq.) showed a F2 segregation ratio 45:9:10 (multiple flowers: intermediate flowering type: single flower) for the inheritance of multiple flowers. The interspecific hybridization, together with the intraspecific hybridization of 'Serrano Chili' crossed with 'Keystone Resistant Giant No. 4', 'Cayenne Large Red', and 'LSU Sport', showed a consistent F2 segregation ratio of 13:3 (pubescent leaf: glabrous leaf) for the inheritance of leaf pubescence.

The epidermis of leaves and floral organs of 'Serrano Chili' and No. 178 were studied with the scanning electron microscope (SEM). Elongated hairs were present in the costal and intercostal regions of both leaf surfaces of 'Serrano Chili', but only in the costal region of No. 178 leaf surfaces. The study on floral organs indicated a similar epidermal morphology between 'Serrano Chili' and No. 178. Elongated hairs and stomata were present on the abaxial surface while...
short glandular hairs densely covered the adaxial surface of a sepal. Hairs were produced at the tip and along the margins of the petal; stomata were found on the abaxial surface of the petal and associated with the "tip-hair-zone". No hair was found on stamens or carpels. Stomata were found on the abaxial surface of the anther lobe and restricted to the area near the connective tissue. On the adaxial surface of the filament base and the abaxial surface of the ovary base, stomata were also found; stomata found in these regions were considered to be related to nectar secretion in pepper flowers.
Chapter I

Inheritance of Multiple Flowers and Leaf Pubescence in
Interspecific Crosses of Capsicum annuum X Capsicum chinense
Abstract

The inheritance of multiple flowers and leaf pubescence resulting from the crosses between pepper species *Capsicum annuum* L. and *Capsicum chinense* Jacq. was examined. Crosses and selfing were made by hand-pollination in a glass greenhouse. Only eight normal F1 plants were obtained from the crosses with *Capsicum annuum* L. as the female parent. F2 and backcross generations obtained from these FIs and two parents were grown in the field, and two field surveys were conducted to evaluate the progeny for the characters under study. The results indicated that multiple flowers and leaf pubescence are controlled by dominant alleles. A 3-gene model leading to a F2 segregation ratio 45:9:10, and a 2-gene model leading to a F2 segregation ratio 13:3 were suggested for the inheritance of multiple flowers and leaf pubescence respectively. Epistasis was employed to interpret the observations. No linkage was found between these two characters. The inconsistencies between F2 and backcross data might be explained by interspecific hybridization. A genetic study based on intraspecific crosses for leaf pubescence supported the 2-gene model leading to a F2 segregation ratio 13:3 (pubescent leaf: glabrous leaf).
Introduction

Although pepper plants have been often studied for agricultural value, the inheritance of certain morphological traits has not been well established (4). As a result of the interest in transferring useful genes from wild-type peppers into widely grown cultivars, it is desirable to have some genetic information about morphological traits.

*Capsicum annuum* L., the most widely grown pepper species in the world, sets a single flower at each node; whereas, *Capsicum chinense* Jacq., a popular pepper species in South and Central America, sets two or three flowers at each node. The character of two or three flowers set at each node was defined as the multiple-flower trait. Multiple flowers may provide a potential to increase yield and to enhance uniform maturity, which conceivably could make mechanical harvesting feasible.

Subramanya (8) reported a possible gene transfer for the multiple-flower trait from *Capsicum chinense* (PI 159236) into *Capsicum annuum* (cv. Delray Bell). He suggested that three major dominant genes may control double flowers at each node, and that additional genes may be involved in the expression of more than two flowers at each node. Tanksley and Iglesias-olivas (9) employed co-segregation of enzyme-coding
genes as markers and concluded that at least five independently segregating chromosomal segments are involved in the multiple-flower inheritance of PI 159234 (crossed with C. annuum cv. NM 6-4). Meanwhile, Greenleaf (1) cited an unpublished conclusion by Watson and Greenleaf that seven additive genes determine the multiple-flower in Capsicum chinense Acc. 1555.

Most pepper genotypes have glabrous leaves with or without pubescence on the abaxial veins, petioles or stems. Two contradicting results were reported regarding the inheritance of leaf and stem pubescence in peppers. Ikeno (3) found that pubescence of stems, petioles, and leaves segregated in a 15:1 F2 ratio, with individuals exhibiting hairs varying in degrees of pubescence. Holmes (2) observed a smooth stem was dominant over a hairy stem.

If we consider the transfer of a useful gene from a wild plant into a cultivated plant, it is possible to simultaneously introduce those genes which are responsible for unacceptable traits. Therefore, it is necessary for pepper breeders to have an understanding of the the genetics of certain morphological traits in Capsicum. The objectives of this study are 1) to examine the inheritance of multiple flowers in Capsicum annuum X Capsicum chinense crosses; 2) to examine the inheritance of leaf pubescence in interspecific and intraspecific hybridizations.
Materials and Methods

In this study, No.178 (from Dr. J. F. Pontenot's pepper selection program, Department of Horticulture, Louisiana State University), was used as the Capsicum chinense parent (P1). No.178 is homozygous for both multiple flowers and glabrous leaf. 'Serrano Chili', which is homozygous for single flower and pubescent leaf, was used as the Capsicum annuum parent (P2).

In the spring of 1986, reciprocal crosses were made between No.178 and 'Serrano Chili' in a glass greenhouse. In the fall of 1986, the F1 seeds were harvested and planted in the same greenhouse. Only eight normal F1 plants were obtained; all eight F1 plants came from the crosses with 'Serrano Chili' as the female parent. Self and backcross pollinations to P1 and P2 were made by hand. In the spring of 1987, two parents, F2, BC1P1 (F1♀ X No.178 ♂), BC1P2 (F1♀ X Serrano Chili ♂), and rBC1P2 (reciprocal BC1P2 = Serrano Chili ♀ X F1 ♂) plants were grown at the Hill Farm located on the Louisiana State University, Baton Rouge campus. A randomized block design with three replications was used. The total plant number grown for each generation was: 60 for each parental species, 117 for BC1P1, 149 for BC1P2, 35 for rBC1P2, and 320 for F2. In the fall of 1987, two field...
surveys were completed for classifying the traits under
study. The first survey was completed after the flower
number at the fifth node could be clearly distinguished.
The second one was completed about one month later.

A study based on the intraspecific hybridization was
conducted in the greenhouse to observe the pubescent leaf
trait. Crosses were made between 'Serrano Chili' and
several cultivars which belong to Capsicum annuum and have
glabrous leaves. These cultivars were: 'Keystone Resistant
Giant No.4' (bell type pepper), 'Cayenne Large Red', and
'LSU Sport'. Two surveys for leaf pubescence were done on
the plants at the seedling stage before stem bifurcation.
Results

F1. Among the reciprocal crosses made between No.178 and 'Serrano Chili', only eight normal F1 plants were obtained from the crosses with 'Serrano Chili' (Capsicum annuum L.) as the female parent. The F1 plants, which are vigorous and morphologically uniform, produced two or three flowers per node and pubescent leaves. All F1 plants from intraspecific hybridizations had pubescent leaves. These observations indicated that the multiple-flower and the pubescent leaf are dominant traits.

Multiple flowers. Results of segregation for multiple flowers are shown in Table 1. In the F2 population, 181 plants had the multiple-flower trait while 37 plants had the single-flower trait. An intermediate flowering type was defined here as: multiple-flowered nodes and single-flowered nodes are almost equally distributed on the same plant. Twenty six plants which showed the intermediate flowering type were obtained.

Based on the F2 population, three major genes designated M1, M2, and M3 were proposed to control the multiple-flower expression in peppers. The genotypes of P1, P2 and F1 are M1M1M2M2M3M3 (multiple-flower), m1m1m2m2m3m3 (single-flower), and M1m1M2m2M3m3 (multiple-flower), respectively. In the
F2 population, M1, determines the expression of multiple flowers when the dominant gene is present at either M2 or M3 locus, or both loci. Recessive homozygosity at M1 locus modifies the expression and reduces the multiple-flowered nodes in spite of the dominant genes present at both M2 and M3 loci. Recessive homozygosity at any two loci is epistatic to the dominant gene present at the third locus. The proposal leads to a F2 segregation ratio of 45:9:10 (multiple-flower: intermediate flowering type: single-flower). A $X^2$ of 2.57 ($P = 0.50-0.25$) indicated that F2 data fit the model. But two BC1P2 populations had deviated segregation from the expected ratio based on the model. The heterogeneity test showed a significant difference between BC1P2 and rBC1P2 populations at the 5% level, but a conclusion was hard to make about the difference because of the small rBC1P2 population (31 plants).

Leaf pubescence. Segregation of the leaf pubescence trait in F2 and backcross generations derived from "Serrano Chili X No. 178" crosses are shown in Table 2. In the F2 population, 207 pubescent leaf and 47 glabrous leaf plants were obtained. Based on the F2 population, a ratio of 13 pubescent leaf to 3 glabrous leaf is apparent; a very good $2 \chi^2$ fit, $X^2 = 0.01$, was obtained. But, a $X^2$ of 6.67 in BC1P1 indicated a poor fit to the suggested model.
Two major genes, H and Sm, were proposed to condition the pubescence on the leaf surface. The genotypes of P1, P2 and F1 are hhSmSm (glabrous or smooth leaf surface), HhSmsm (pubescent leaf surface, typical of 'Serrano Chili') and HhSmsm (pubescent leaf surface), respectively. Gene pair H controls the pubescent leaf expression and is dominant for the pubescent leaf of 'Serrano Chili' while gene pair Sm controls the smooth leaf expression and is dominant for the glabrous leaf of No.178. H is epistatic to Sm while smsm is epistatic to hh. In the F2 population, the combinations of H_Sm, H_smsm and hhsmm have pubescent leaves and the hhSm has glabrous leaves.

The results of crossing 'Serrano Chili' with 'Keystone Resistant Giant No. 4', 'Cayenne Large Red', and 'LSU Sport' indicated that the F2 data from three intraspecific crosses supported the observation on the inheritance of the pubescent leaf in the interspecific hybridization (Table 3). The goodness of fit for testcross data from F1 of "Serrano Chili X Cayenne Large Red" backcrossed to 'Cayenne Large Red' was consistent with a 1:1 expected ratio.

2 Linkage. The X test was used to determine whether the characters under study segregate independently. The results based on the F2 data are shown in Table 4. A good fit of X of 4.31 for independent segregation of multiple flowers and leaf pubescence was obtained.
Discussion and Conclusions

Although the majority of F1 seeds from interspecific crosses did not germinate, or the seeds germinated but produced abnormal plants, eight normal plants were obtained. It was not difficult to use the F1 plants to produce F2 and backcross progeny which was used in this study. Some early reports dealing with interspecific hybrids indicated the difficulty to obtain viable F1 seeds and good F2 progeny (5, 6, 7). In interspecific hybrids, deviation from the normal Mendelian segregation is not uncommon (5, 6, 7, 9). Such deviation also occurred in the segregating generations of "Serrano Chili X No. 178" crosses and was reflected by the observed inconsistencies between F2 and backcross populations.

Inheritance of multiple flowers. In a F2 population of 244 plants, 181 plants exhibited the multiple-flower trait. Subramanya (8) classified 54 plants as the double-flower and one as the single-flower type among his 55 F2 individuals. Although his population was too small to draw a definite conclusion, the data suggested that the double-flower phenotype was easy to recover in the F2 generation. Tanksley and Iglesias-olivas (9) indicated that the F2 population was skewed toward the Capsicum annuum parent based on the mean
flower number per node (1.37 flowers per node, i.e., more F2 plants had single flower). Based on the F2 data of this study, the skew was toward the Capsicum chinense parent (74% multiple-flowered plants in the F2 population).

Subramanya (8) suggested a 3-gene model (F2 segregation ratio of 63:1) for the double-flower expression in peppers and concluded that additional genes modified the multiple-flower trait. Tanksley and Iglesias-olivas (9) found that at least five independently segregating chromosome segments were involved in the multiple-flower expression according to the co-segregating data of enzyme-coding genes and epistasis played an important role. Greenleaf (1) mentioned that seven additive genes determine the multiple-flower trait in Acc. 1555. A 3-gene model with epistasis was proposed to explain the genetic control of multiple flowers in No. 178. The F2 data obtained in this study fit a 45:9:10 F2 segregation ratio.

The difficulty of explaining the BC1P2 by the suggested model is very significant. Previous investigations on other crops reported that selective elimination favored the recurrent parent genotype in interspecific backcrosses (5, 6, 7). Subramanya (8) and Tanksley and Iglesias-olivas (9) also observed the deviation from the normal Mendelian segregation in the progeny of interspecific crosses of C. annuum X C. chinense.
In this study, BC1P2 populations favored the recovery of single-flowered plants (32% higher than the expected number of single-flowered plants) and showed a severely selective elimination of multiple-flowered plants (84% lower than the expected recovery). These BC1P2 data may imply that multiple-flower genes are located on the chromosomes which are easily eliminated in interspecific backcrosses. From the standpoint of breeding, early selection in a F2 population may be an acceptable method to introduce the multiple-flower genes into commercial cultivars, as was suggested by Tanksley and Iglesias-olivas (9).

Inheritance of leaf pubescence. Ikeno (3) reported that pubescent stems, petioles, and leaves in peppers had a 15:1 (pubescent: glabrous) F2 segregation ratio with individuals in dominant pubescent class exhibiting different degrees of pubescence. Holmes (2) observed that the smooth stem is dominant over the hairy stem. The results in this study agree with those of Ikeno's which indicated that a dominant pubescence and two-gene controlling mechanism but disagree with his 15:1 segregation ratio. In the F2 generation of "Serrano Chili X No. 178", a 13:3 (pubescent leaf to glabrous leaf) segregation ratio was found; but, the gene model supported by the F2 ratio couldn't explain the BC1P1 (testcross for pubescent leaf trait) segregation. More
pubescent leaf plants recovered in BC1P1 implied a selective advantage of 'Serrano Chili' genotype deviating from the usual observation of selective elimination of donor-parent genotype. This is probably caused by segregation and recombination of some modifier gene(s) originating in the 'Serrano Chili' parent but not linked with the major pubescent leaf genes, or some unidentified genetic mechanism related to No.178 leaf phenotype. Plants of No. 178 have shiny, glabrous (or smooth), and wavy wrinkled leaf surface but a short type of hairs on their stems and leaf veins (particularly abaxial veins). Therefore, the same pubescence genotype in BC1P1 may express a glabrous leaf surface when the modifiers are lacking but a pubescent leaf surface when the modifiers are present.

The results from the intraspecific hybridization supported the gene model suggested by the interspecific cross. Three F2 populations all showed a 13:3 (pubescent to glabrous) ratio. One testcross of "Serrano Chili X Cayenne Large Red" backcrossed to 'Cayenne Large Red' was obtained; the segregation ratio (1:1) in the testcross fits the suggested gene model.

An interesting phenomenon noted was that different degrees of pubescence appeared not only among individuals within the F2 population but also between F2 populations. The gene model
proposed for leaf pubescence assumes that \( H_\) (pubescence) was epistatic to \( Sm_\) (smooth) and \( smsm_\) (pubescence) was epistatic to \( hh_\) (smooth). The dominance and epistasis may not be complete, thus different degrees of pubescence are common within the population. Among different F2 populations, the F2 population derived from "LSU Sport X Serrano Chili" had a majority of plants with 'Serrano Chili' type of pubescence compared to the other populations. This leads to a speculation that there are possibly multiple alleles existing among the different pepper cultivars with glabrous leaves.

In this study, the gene transfer of the multiple-flower trait was confirmed and a gene model for its inheritance was hypothesized. No linkage was found between multiple flowers and leaf pubescence; therefore, multiple flowers can be introduced into some cultivar, e.g. 'Serrano Chili' without changing its original leaf types. On the other hand, because the selective elimination of multiple-flowered plants occurred in the interspecific backcross population, an early F2 selection is a favored breeding strategy.

In addition, the gene model for leaf pubescence was proposed based on both interspecific and intraspecific hybrids data. The intraspecific F2s and backcrosses were included with the hope to avoid the disadvantage derived from the
interspecific hybridization, such as the deviation from the normal Mendelian segregation ratio in F2 or backcross populations. The results for leaf pubescence in two hybridizations were consistent. This may suggest that the genetic combinations in the F2 population of "Serrano Chili X No. 178" can serve to predict the genetic models for the characters of these two varieties.
Table 1. Segregation frequency of multiple flowers in F2 and backcross generations derived from the cross between 'Serrano Chili' and No.178.

<table>
<thead>
<tr>
<th>Generation</th>
<th>Total</th>
<th>Observed</th>
<th>Tested</th>
<th>Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>F2</td>
<td>244</td>
<td>181</td>
<td>26</td>
<td>37</td>
</tr>
<tr>
<td>BC1P1</td>
<td>102</td>
<td>99</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>BC1P2</td>
<td>121</td>
<td>8</td>
<td>11</td>
<td>102</td>
</tr>
<tr>
<td>rBC1P2</td>
<td>31</td>
<td>1</td>
<td>7</td>
<td>23</td>
</tr>
<tr>
<td>BC1P2(pooled)</td>
<td>152</td>
<td>9</td>
<td>18</td>
<td>125</td>
</tr>
</tbody>
</table>

z BC1P1 = F1♀ X P1♂, BC1P2 = F1♀ X P2♂, rBC1P2 = P2♀ X F1♂.

y MF = multiple flowers, SF = single flower, MS = multiple-flowered nodes and single-flowered nodes are almost equally distributed on the same plant.

NS, *** Nonsignificant (NS) or significant at 0.1% level, respectively.
Table 2. Segregation frequency of leaf pubescence in F2 and backcross generations of the cross between 'Serrano Chili' and No.178.

<table>
<thead>
<tr>
<th>Generation</th>
<th>Plants</th>
<th>Total</th>
<th>Observed</th>
<th>Test Ratio</th>
<th>NS, **</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F2</td>
<td>254</td>
<td>207</td>
<td>47</td>
<td>13:3</td>
<td>0.01 **</td>
</tr>
<tr>
<td>BC1P1</td>
<td>100</td>
<td>63</td>
<td>37</td>
<td>1:1</td>
<td>6.76</td>
</tr>
<tr>
<td>BC1P2</td>
<td>123</td>
<td>123</td>
<td>0</td>
<td>----</td>
<td>----</td>
</tr>
<tr>
<td>rBC1P2</td>
<td>30</td>
<td>30</td>
<td>0</td>
<td>----</td>
<td>----</td>
</tr>
<tr>
<td>BC1P2(pooled)</td>
<td>153</td>
<td>153</td>
<td>0</td>
<td>----</td>
<td>----</td>
</tr>
</tbody>
</table>

z BC1P1 = F1 ♀ X P1 ♂, BC1P2 = F1 ♀ X P2 ♂, rBC1P2 = P2 ♀ X F1 ♂.

y P = pubescent leaf, G = glabrous leaf.

NS, ** Nonsignificant (NS) or significant at 1% level.
Table 3. Segregation frequency of leaf pubescence in three intraspecific F2 populations and one testcross population.

<table>
<thead>
<tr>
<th>Generation</th>
<th>Observed plant number</th>
<th>Test ratio</th>
<th>z</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>P</td>
<td>G</td>
<td>X</td>
</tr>
<tr>
<td>F2 (Serrano Chili x</td>
<td>112</td>
<td>91</td>
<td>21</td>
</tr>
<tr>
<td>Resistant Giant No.4)</td>
<td>NS</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F2 (Serrano Chili x z Cayenne</td>
<td>28</td>
<td>23</td>
<td>5</td>
</tr>
<tr>
<td>Large Red)</td>
<td>NS</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F2 (Cayenne Large Red z x</td>
<td>100</td>
<td>83</td>
<td>17</td>
</tr>
<tr>
<td>Serrano Chili)</td>
<td>NS</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Testcross</td>
<td>134</td>
<td>69</td>
<td>65</td>
</tr>
<tr>
<td>F2 (LSU Sport x</td>
<td>189</td>
<td>153</td>
<td>36</td>
</tr>
<tr>
<td>Serrano Chili)</td>
<td>NS</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

z These two F2s were from reciprocal crosses, we considered them as one cross although data were not pooled.

y P = pubescent leaf, G = glabrous leaf.

x Testcross = (Serrano Chili x Cayenne Large Red) x Cayenne Large Red.

NS Nonsignificant.
Table 4. Independent segregation in F2 population for multiple flowers and leaf pubescence.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Frequency</th>
<th>Expected value</th>
<th>Total</th>
<th>$X$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>M-P</td>
<td>147</td>
<td>152.45</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MS-P</td>
<td>24</td>
<td>22.01</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S-P</td>
<td>32</td>
<td>28.53</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M-G</td>
<td>40</td>
<td>34.55</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MS-G</td>
<td>3</td>
<td>4.99</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S-G</td>
<td>3</td>
<td>6.47</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>----</td>
<td>---</td>
<td>----</td>
<td>249</td>
<td>4.31</td>
<td>0.75-0.50</td>
</tr>
</tbody>
</table>

$z$ M = multiple flowers, MS = intermediate flowering type, S = single flower, P = pubescent leaf, G = glabrous leaf.
Literature Cited


Chapter II

A Morphological Investigation

on

the Leaf Surfaces and Floral Organs

in *Capsicum annuum* L. and *Capsicum chinense* Jacq.
Abstract

The epidermis of leaves and floral organs of 'Serrano Chili' (Capsicum annuum L.) and No. 178 (Capsicum chinense Jacq.), and the leaf epidermis of the F1 plants of "Serrano Chili X No. 178" were studied with the scanning electron microscope (SEM). Elongated hairs were present in the costal and intercostal regions of both leaf surfaces of 'Serrano Chili', but only in the costal region of No. 178 leaf surfaces. When F1 leaves were looked by naked eyes, they had 'Serrano Chili' appearance. Anyhow, based on the examination with SEM, 'Serrano Chili' contributed the "abundance" and the "elongation" while No. 178 contributed the "hair-type" to their F1 progeny. The study on floral organs indicated a similar epidermal morphology between 'Serrano Chili' and No. 178. Elongated hairs and stomata were present on the abaxial surface while short glandular hairs densely covered the adaxial surface of a sepal. Hairs were produced at the tip and along the margins of the petal; stomata were found on the abaxial surface of the petal and associated with the "tip-hair-zone". No hair was found on stamens and carpels. Stomata were found on the abaxial surface of the anther lobe and restricted to the area near the connective tissue. On the adaxial surface of the filament base and the abaxial surface of the ovary base, stomata were also found; stomata
found in these regions were considered to be related to nectar secreting in pepper flowers.
Introduction

The morphological features are usually characteristic of a given plant organ and are typical of a given taxon. The epidermal features of a plant organ can be considered to reflect its specific function and adaptation to a certain environment. For example, Gale and Owen (1983) suggested that the epidermal features of floral organs is of use not only in classification but also in respect of determining the mechanisms of floral protection and pollinator attraction.

The interests in more detailed observation on the epidermis of a plant organ have been encouraged by the development and improvement of electron microscopes, particularly the scanning electron microscope (SEM). By using SEM, we can examine the variations in stomatal structures, hair types, surface sculpturing of epidermal cells, and the presence or absence of stomata or hairs.

In a series of pepper breeding projects, the insignificant flowers of Capsicum species, and an unique leaf type of one variety 'Serrano Chili', attracted the attention for a detailed study about their epidermal morphology.

Solanaceae, which is one of the heterogeneous families in the plant kingdom, has many members that are important economic
crops. The genus *Capsicum* is one of them. The species *Capsicum annuum* L. is the most popular pepper species grown in the world and its fruits have long been used for food and medicine.

The flower morphology of *Capsicum* has been studied much less frequently in comparison with some other genera (e.g., *Lycopersicon*, *Nicotiana*, *Petunia*, or *Solanum* etc.) in the same family. When new genetic materials from wild species are introduced into the domesticated peppers or when the mutants associated with fertility are used in breeding projects, a botanical understanding of the pepper flower becomes increasingly required.

The objective of this study is to examine the epidermis of the leaf and the floral organs of two closely related pepper species, *Capsicum annuum* L. and *Capsicum chinense* Jacq., by using the scanning electron microscope (SEM). It is hoped that this study can clarify the confusion about some structure-function relationships in peppers and it is also hoped that the better understanding about a pepper flower will offer a solid basis for further breeding projects on this plant.
General morphology on the plant epidermis

The specialized epidermal cells such as the guard cells (of a stoma) and various types of trichomes, associated with the configurations of the cuticle layer over the outer cell walls of the epidermis, play an important role in the morphology of a given plant organ. The diversification in the epidermal morphology also reflects the structure-function relationship in a specific environment.

The guard cells, together with the opening limited by them, form the "stoma". Stomata can be found on all aerial parts of the plant, but they are most abundant on the lower surface of the leaf (Esau, 1977). The stomata on petals, stamens, carpels or seeds are usually considered "non-functional" (Fahn, 1982). The roots (except rhizomes) have been thought to lack stomata (Esau, 1977; Fahn, 1982), but recently, it was found that the roots do have stomata (Lefebvre, 1985; Christodoulakis and Psaras, 1987; Tarkowska and Wacowska, 1988).

The stomata on roots were first discovered in the root hair zone of the seedling roots of Helianthus annuus (by Tietz and Urbasch, 1977, cited by Christodoulakis and Psaras, 1987, and
Then, in *Pisum sativum* L., both open and closed pores were found in the region 10-30 mm from the cotyledons on the primary root (Lefebvre, 1985). The stomata in *Pisum* had a patchy distribution and in some instances, were closely associated with root hairs.

In *Ceratonia siliqua* (a carob tree), stomata were randomly distributed throughout the surface of the root zones which had mature vascular tissues, i.e., from the root-hair-zone to transitional zone (Christodoulakis and Psaras, 1987). Within the root-hair-zone, again, hairs are often closely associated with the guard cells.

In a more detailed investigation on the primary roots of *Helianthus annuus* L., *Pisum arvense* L. and *Ornithopus sativus* L., Tarkowska and Wacowska (1988) indicated that the stomata in the root-hair-zone do not have normal stomatal function. The characteristics of the stomata from the root hair zone --- absence of chloroplasts, lack of the marked thickness of the cell wall and lack of sensitivity to ABA --- showed that they cannot fulfil the role of normal stomata. On the other hand, above the root-hair-zone, functional stomata increased toward the cotyledons. Because the stomata in the root-hair-zone were always open, therefore, they were suggested to function as part of the root aeration system although they might not have normal stomatal function.
Stomata may be even with, raised above, or sunken below the other epidermal cells. Sunken stomata are common in xerophytes, but raised stomata are much less reported.

Raised stomata were found in the region above the root-hair-zone on the primary roots (Christodoulakis and Psaras, 1987; Tarkowska and Wacowska, 1988). In C. siliqua, the stomata on the root were raised although those on the leaf were sunken (Christodoulakis and Psaras, 1987). On Coleus (Lamiaceae) stems, raised stomatal clusters occurred on internodes but were absent from nodes (Turner and Lersten, 1983). According to Turner and Lersten, the raised-stoma-clusters on Coleus occurring on the plants grown in relatively dry, as well as in relatively moist environments suggested that the elevation of the stomata is a normal, genetically determined feature.

Morphologically, several main types of stomata have been distinguished in dicotyledons on the basis of the arrangement of the epidermal cells neighbouring the guard cells. They are described as: (1) anomocytic (irregular-celled) - no subsidiary cells are present; (2) anisocytic (unequal-celled) - three subsidiary cells, one distinctly smaller than the other two; (3) paracytic (parallel-celled) - one or more subsidiary cells accompany the stoma on either side, the long axis of subsidiary cells parallel to that of guard cells; (4) diacytic
(cross-celled) - two subsidiary cells with their common wall at right angles to the guard cells are present; (5) actinocytic (radiate-celled) - a circle of radiating cells are present to surround the stoma (Metcalfe and Chalk, 1950).

One or more stomatal types may be characteristic of a given taxon and may be of significance in taxonomy. The normal and mature leaves of 28 species in Solanum (Solanaceae) have been studied; stomata were either of the anisocytic type, or both the anisocytic and anomocytic types found in the same species (Ahmad, 1964).

On the basis of the epidermis in 56 species belonging to 45 genera of Solanaceae, almost all stomatal types described in the Dicotyledons could be recognized in this family (Bessis and Guyot, 1979). Solanaceae could be divided into two series: one is homogeneous and has mainly anisocytic stomata and the other is heterogeneous and has different types of stomata. Besides these, all species studied have perigenous anomocytic stomatal types and the first stomata to appear are always of this type.

In addition to stomata, epidermal cells may differentiate into unicellular or multicellular appendages which are so-called 'trichomes'. The trichomes include various types of hairs, papillae, or scales (Esau, 1977; Fahn, 1982). The various types of hairs --- glandular or non-glandular, unicellular or
multicellular, branched or unbranched — are sometimes remarkably uniform in a given taxon and can be used for taxonomic purposes. In some cases, whole family can be easily recognized by the occurrence of one or more distinctive hair types while in other cases, hairs are of more value for determining genera or species (Matcalfe and Chalk, 1950), or for analysing interspecific hybrids (Fahn, 1982).

Although the functions of various types of trichomes are still not well established, some of them have been suggested. In Solanum, a type of glandular hair which consists of a four-lobed (four-celled) head mounted on a stalk was found abundant in three wild potato species but scarce in the cultivated potato (S. tuberosum cv. Arran Pilot) (Gibson, 1971). These hairs could discharge an exudate which initially impede aphids' movement and further accumulation eventually caused aphids to stick to the plants. Furthermore, this hair type was considered to be transferable from the wild potatoes into the cultivated potatoes (Gibson, 1974).

This glandular hair type was also found in cultivated potato, S. tuberosum L. cv. Russet Burbank, too (McCuauley and Evert, 1988). Short, simple and teethlike marginal trichomes and simple, uniseriate, and multicellular (two- to four-celled) hairs of varying lengths were also seen on the leaves of this cultivar. Whereas the adaxial trichomes were found mainly on the ribs, the
abaxial trichomes were found both on the ribs and scattered across the surface.

One distinguishing feature of the epidermis is its outer cell walls and the presence of a thin continuous layer of predominantly lipid materials deposited on its outermost surface. The latter layer is termed as "cuticular membrane" by Holloway (1982) or "cuticle" by many other scientists. Chemically, this layer can be characterized by two specific lipid groups: insoluble polymeric "cutins" and soluble "waxes". The cutins constitute the framework of the cuticle while the waxes constitute the "epicuticular wax" deposited on the surface and the "cuticular wax" embedded within the cuticle layer (Holloway, 1982).

Three orders of surface sculpturing can be defined in the studies of the Aloe leaf epidermis: (1) the outlines of individual cells; (2) the outer wall of epidermal cells --- may be flat, slightly domed, strongly domed but with a prominent central papilla, or slightly concave; (3) the superimposed finer structures such as the fine (small) micropapillae, moderately coarse micropapillae, or coarse micropapillae (Cutler, 1982).

It was shown that the leaf surface morphology is under precise genetic control (Brandham and Cutler, 1978); some cuticular characteristics are typical of the closely related species and these are particularly found when the species from
extreme habitats are compared. The correlation between surface sculpturing and habitat is quite strong (Cutler, 1932).

On the other hand, the morphology of epicuticular wax may be modified by environmental conditions although it is also considered under genetic control (Baker, 1982). The wax alteration occurred during electron microscopy preparation (Reed, 1982), but the SEM (scanning electron microscopy) images of the epidermal surface sculpturing appeared stable through different preparation procedures (Cheng et al., 1979).

Morphology of floral organs

Little work has been done on the morphology of floral organs in comparison with that of leaves or stems except for the stigma of angiosperms. The surface features of the stigmas of angiosperms have been thoroughly examined because they are involved in controlling breeding systems and particularly in regulating the self-incompatibility (Heslop-Harrison and Shivanna, 1977).

The interest in studying the morphology of other floral organs has increased recently. The development and improvement of electron microscopes, particularly the scanning electron microscope, may be the major reason for the increased interest; the detailed observations on the surface features of floral organs become very easy and the results are very good.
According to Heslop-Harrison et al. (Heslop-Harrison and Shivanna, 1977), the principal subdivision is into stigmas of the "dry" type, with little or no surface secretion at maturity, and the "wet" type, with a free fluid surface where a distinct surface secretion is present. Within the "dry" and "wet" categories, the taxa can be further classified into "smooth, non-papillate" type and "papillate" type.

In the family Solanaceae, most genera (e.g., Lycopersicon, Nicotiana, Petunia, and Solanum etc.) have "wet" stigmas and receptive cells with low to medium papillae (Heslop-Harrison and Shivanna, 1977). The stigma of the pimiento pepper (Capsicum) flowers was reported to be slightly bulbous and lobed; the stigma surface was papillate and covered with a rather viscous fluid (Cochran and Dempsey, 1966).

The investigations on the stigmatic structure showed a close similarity between the stigma of Petunia hybrida (Konar and Linskens, 1966) and that of Lycopersicon peruvianum Mill. (Dumas, et al., 1978), Lycopersicon esculentum Mill. (Kadej et al., 1985), Nicotiana tabacum L. (Cresti, et al., 1986), and Nicotiana sylvestris Speg. and Comes (Kandasamy and Kristen, 1987). In these species, the epidermis of a mature stigma differentiates into one- or two-celled hairs or papillae. A thin cuticle layer covers the surface of the young stigma; at maturity, the exudate
accumulates between the cuticle and the outer cell wall of the papillae. The cuticle is finally ruptured and the exudate spreads over the stigma surface. Several subepidermal cell layers form "the secretory zone" or "the glandular zone". The intercellular spaces of the secretory zone are large, many, and filled with secretory products at maturity. The cells below the secretory zone and downwards into the style are parenchyma; the elongated cells of the transmitting tissue merge into the secretory zone forming an intercommunicating system. The components of the exudate over the stigma surface and in the intercellular spaces of the secretory zone are not consistent in these species, but the exudate is always rich in lipids.

The transmitting tissue of the style of Nicotiana tabacum L. (cv. Wisconsin 38) was revealed to be comprised of narrow, elongated cells separated by massive amounts of densely-stained amorphous materials (Bell and Hicks, 1976). In Lycopersicon peruviam Mill., the pollen tube pathway was found to be a continuous tract of mucilage from the stigma surface to the ovule micropyles (Webb and Williams, 1988). The mucilage was presumed to represent the secretory products of the adjacent specialized cells of the transmitting tissue. The mucilage on the stigma is rich in lipids while the mucilage in the style and ovary is rich in arabinogalactans. The style of Lycopersicon has a thick
crenulate cuticle and an epidermis with stomata. The green chloroplasts were found in the transmitting cells of both Nicotiana (Bell and Hicks, 1976) and Lycopersicon (Webb and Williams, 1988); according to these authors, the chloroplasts in the transmitting tissue suggested a photosynthetic activity that would alleviate the necessity of "importing" food materials from the other common photosynthetic sites.

The epidermal cells of the style are more or less elongated and oriented along the axis of this structure (Gale and Owens, 1983; Chandra Sekhar and Sawhney, 1984; Polowick and Sawhney, 1986). On the stylar surface, the cuticular ridges (or thickenings) are prominent and parallel to the long axis of the epidermal cells and they terminate at the base of the stigma.

In tomato flowers (Lycopersicon esculentum Mill., cv. Pearson), hairs were present on the lower half of the style while stomata were restricted to the distal region of this structure (Chandra Sekhar and Sawhney, 1984). Raised stomata were found on the young style. The hairs, stomata, and cuticular thickenings were absent on the ovary.

In Brassica napus (cv. Westar), no hairs were found on any of the floral organs. Stomata were interspersed throughout the stylar surface. The ovary wall was composed of irregular-shaped epidermal cells and contained no stomata (Polowick and Sawhney, 1986).
Two distinctive zones were perceived in the wall of a mature ovary or the pericarp of a young fruit in *Capsicum annuum* L. (Munting, 1974). The upper two-thirds to three-quarters of the ovary wall or the pericarp had the cells with a parietal cytoplasm and one central vacuole. The remaining lower part had protoplasma-rich cells with small vacuoles and was considered to be meristematic during anthesis and part of post-anthesis. The fruit growth was irregular; the developing fruits of *Capsicum annuum* grew most rapidly at the base.

Although they mentioned the nectar-secreting by the ovary or by the nectaries located at the base of ovary in some genera of Solanaceae, Martin et al. (1932) did not find any indication that the ovary of the genus *Capsicum* functions as a nectary. According to these authors, in the genus *Capsicum*, the nectar is secreted by the basal portion of the corolla tube. The grooves on the inside of the corolla tube and between the filaments, and the duck-like spaces between the backs of the filaments and the corolla tube are the places for secreting and conducting nectar. The inner epidermis of the corolla-filament tube, because of its formation of much mucilage, participates most noticeably in the secretory process. The parenchyma of the corolla-filament tube apparently contributes some of the sugar in the nectar through the conversion of the starch it holds in storage, while it is
probable that the vascular bundles of the corolla-filament tube contribute sugar directly from the transportation stream.

In a more complete study on the flower morphology of Solanaceae, the nectaries of all species examined were at the base of the gynoecium (or ovary) or on its base except for *Solanum luteum* and *Nierembergia frutescens* (Huber, 1980). Even in the genus *Capsicum*, a ring-shaped nectary gland was found to differentiate at the base of the ovary.

Cuticular thickenings were found on the stamens of *Zea Mays* (Cheng, et al., 1979), Commelinaceae (Gale and Owens, 1983), *Lycopersicon* (Chandra Sekhar and Sawhney, 1984), and *Brassica* (Polowick and Sawhney, 1986).

In male-fertile corns (*Zea Mays* L.), at about the 63-day stage, a ridged cuticle developed and formed quickly on the outer epidermal wall of the anthers (Cheng et al., 1979). In a genic male-sterile corn (ms10), the anther epidermis began to develop ridges at about the same stage and this process did never complete. These ridges were primarily oriented parallel to the long axis of the epidermal cells and continuous from cell to cell. It was assumed that the cuticle development probably forms a rigid anther-wall which gives the additional force to accomplish the anther dehiscence.
A SEM study revealed that four rows of hairs, two lateral and two adaxial, are responsible for the lateral cohesion of tomato anthers occurring near anthesis (Chandra Sekhar and Sawhney, 1984). On the abaxial surface, the shapes of the epidermal cells and the cuticular thickenings were different at the terminal, the median and the basal regions of the anther. Stomata were not observed on any part of the stamens in tomato flowers.

In *Brassica napus* (cv. Westar), the mid-rib cells were found strikingly larger than the adjacent cells on the abaxial surface of the mature anther (Polowick and Sawhney, 1986). The cells near the mid-rib base were bulbous while those towards the distal end were more elongate. Stomata were present on the abaxial surface of the anther, but were restricted to the area immediately surrounding the mid-rib cells and especially near the tip of the anther.

In the 'stamenless-2' (*s12/s12*) mutant of tomato, temperature has a dramatic effect on the differentiation of surface features of stamens (Sawhney and Polowick, 1986). Under low temperatures (18 C day / 15 C night), all surface features of mutant stamens closely resembled the normal, whereas under high temperatures (28 C day / 23 C night), the surface features were similar to those of a gynoecium --- a different sex organ.
In the 'ogu' CMS (cytoplasmic male sterility) line of *Brassica napus* L., the stamens exhibited different patterns of differentiation in response to temperature but were not fertile under any conditions (Polowick and Sawhney, 1987). Under high temperatures (28 C day / 23 C night), the abaxial surface of the CMS anther was similar to that of the normal 'Westar' cultivar. Under intermediate temperatures (23 C day / 18 night), most stamens had features of both stamens and carpels. Under low temperatures (18 C day / 15 C night), carpelloid stamens were observed. These carpelloid stamens had not only a stigma surface which consisted of papillate cells identical with the normal stigma, but also the surface features resembling the normal style and ovary.

In the species of Commelinaceae which were studied by Gale and Owens (1983), two major groups were separated based on the characters of petals. The micropapillate epidermal cells with smooth cuticle were typical of one group while the low-domed epidermal cells with striated cuticle and epicuticular wax on their abaxial surface were typical of the other group. Gale and Owens (1983) concluded that the micropapillae and cuticular striation are specific adaptations evolved by these petals to enhance the capture of UV light for utilizing the maximum effects of the pigments.

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The observations on tomato flowers by Chandra Sekhar and Sawhney (1984) revealed that the stomata were present on both surfaces of sepals and only on the abaxial surface of petals. The abaxial surface of young sepals had raised stomata. Cuticular ridges were found only on the abaxial surface for both sepals and petals. Furthermore, the hairs were produced on both surfaces of petals and sepals although the types and frequencies are different. Both sepals and petals had the glandular hairs with club-shaped stalks bearing four lobed glands, while only the abaxial surface of sepals produced the long, multicellular, non-glandular hairs mounted on large foot cells.

In *Brassica napus* (cv. Westar), stomata were observed on both surfaces of sepals but not on petals, while cuticular thickenings were obvious on both surfaces of petals but not on sepals (Polowick and Sawhney, 1986). On the adaxial epidermal cells of petals, the periclinal wall was raised to form a cone and a heavy concentrated thickening was at the tip of the cone but radiated to the edges of the cell. This cell pattern was suggested to absorb incident light efficiently. Two nectaries were located between the filaments of each pair of long stamens. Stomata were confined to the tip of a mature nectary.
Materials and Methods

Different varieties of Capsicum annuum L. and Capsicum chinense Jacq. were continuously grown in a glass greenhouse in 1987 and 1988. The variety 'Serrano Chili' of C. annuum L. and one breeding line 'No. 178' of C. chinense Jacq. (used and maintained in Department of Horticulture, Louisiana State University) were chosen for studying the epidermal morphology of leaves and flowers. The leaves of F1 plants of "Serrano Chili X No. 178" were also included for studying the leaf pubescence.

In the hot summer, the temperature set for the cooling system in the greenhouse was 27 C, although the recorded temperatures usually fell between 35 C (day) and 23 C (night). No artificial light was used at any time. The plants were watered daily and were fertilized or sprayed when needed.

Fully expanded leaves, mature flower buds, and the flowers at anthesis were collected and preserved in a formalin-acetic acid-alcohol (FAA) solution (Sass, 1958) until used. The samples used for the scanning electron microscope (SEM) study were dehydrated through an ethanol series and dissected when they were transferred to 95% ethanol. The dehydrated samples were critical-point-dried with CO2 in a Denton DCP-1 apparatus,
mounted on stubs and coated with gold-palladium in a Hummer I sputter coater. The SEM micrographs were taken on Kodak Tri-X Ortho film with a Hitachi S-500 at 25 KV. The external (abaxial) and internal (adaxial) surfaces of leaf pieces and floral organs were examined in this study.

The buds used for the histological study were dehydrated through a tertiary butyl alcohol series (Sass, 1958) and were embedded in Paraplast. The sections were cut at 8 um thickness and stained with Safranin-fast green.
Results

(I) Leaf epidermal morphology

Serrano Chili. 'Serrano Chili', which is a commercial pepper variety and belongs to the species Capsicum annuum L., has an unique leaf type. The leaf of this variety is lanceolate, whitish-green, and pubescent (very hairy). The SEM study showed that the adaxial surface (Fig. 1) of 'Serrano Chili' is more densely covered by hairs than the abaxial surface (Fig. 2).

Two kinds of hairs were found on both surfaces of this variety: one is elongated, non-glandular and the other is short, glandular. The non-glandular hair is multicellular and uniseriate (Fig. 6, 7); the glandular hair has a multicellular head mounted on a stalk (Fig. 7). On the abaxial surface (Fig. 2), elongated hairs were seen most in the costal regions (the epidermis over the vascular bundles) while the glandular hairs were found scattered in the intercostal regions. Elongated hairs were also abundant along the leaf margins (Fig. 5, 6) with the hairs in the area near the tip having an enlarged basal cell or cells (Fig. 6, at arrows). The elongated hairs were produced through whole adaxial surface making the glandular hairs almost not visible (Fig. 1).
The stomata were typical of anomocytic (Fig. 4) or anisocytic (Fig. 3) type. They were small, numerous, and distributed through whole the abaxial and the adaxial surfaces.

The epidermal cells on both surfaces had sinuous outlines and slightly convex outer walls (Fig. 3, and 4). The cuticle was smooth.

No. 178. 'No. 178', which is a breeding line grown and maintained in Department of Horticulture, Louisiana State University, belongs to the species Capsicum chinense Jacq.; this pepper line has ovate and shiny green leaves. The 'No. 178' leaf surfaces are wavy and glabrous except the epidermis over the major vascular bundles; the epidermis of the large veins produce hairs, particularly in the region near the leaf base. The hairs on the leaf were evident in the SEM micrographs for the adaxial surface (Fig. 8) and the abaxial surface (Fig. 9). The types of glandular hairs and non-glandular hairs of 'No. 178' are similar to those of 'Serrano Chili'; however, the elongated hairs of 'No. 178' seem not as long and soft as those of 'Serrano Chili'. The elongated hairs with slight branching were also seen in the costal region of the adaxial surface (Fig. 8; Fig. 11, at arrows). Short glandular hairs were present on both surfaces (Fig. 8; Fig. 9, at arrows) but more abundant along the small veins of the abaxial surface (Fig. 9, at arrows). Among both non-glandular
and glandular hairs, some were seen having an enlarged basal cell and being produced on a multi-celled base (Fig. 10, at arrows).

The stomata were anomocytic or anisocytic, numerous, and small. The stomata were present on both leaf surfaces but more abundant on the abaxial side. The outlines of the epidermal cells were sinuous and the outer walls were slightly convex; the cuticle was smooth.

_F1._ The F1 plants were obtained from the cross between 'Serrano Chili' and 'No. 178' with 'Serrano Chili' as the female parent. The leaves of F1 plants had a typical 'Serrano Chili' leaf appearance when they were grown in the greenhouse. The SEM study showed that the hairs were present on the adaxial surface (Fig. 12) and the abaxial surface (Fig. 14) of the F1 leaf. The hairs produced in the intercostal regions of the adaxial surface were shorter than those in the costal regions (Fig. 12); the former hairs had an enlarged basal cell (Fig. 12, at arrows; Fig. 13) and elongated acuminatingly towards their tips. The enlarged basal cells were also seen at the base for some "longer" elongated hairs on both leaf surfaces (Fig. 12; Fig. 14, at arrows). The short glandular hairs were abundant on the abaxial surface of F1 leaf (Fig. 14).
(II) Epidermal morphology of floral organs

The flowers of 'Serrano Chili', 'No. 178', and other pepper varieties are pentamerous although the hexamerous and heptamerous flowers are not uncommon. The flowers are actinomorphic, hermaphrodite, and hypogynous. The anthers are tetrasporangiate with two locules in each of two anther lobes. Each ovary has two or three locules with the ovules borne on the placental tissue.

Floral organs of a pepper flower are arranged in the order of, acropetally, sepals, petals, stamens (anther and filament), and carpels (stigma, style and ovary). The lower parts of the adjacent petals fuse to form a "tube" from which arise the free acuminate lobes. And then, the base of each filament fuses with the "corolla tube".

Before anthesis, the petals are interlocked together by the hairs (trichomes) on their tips and margins. On the day of anthesis, the flower opens in the morning but the anthers usually do not dehisce until noon. The flowers used in this study were chosen when their anthers had not dehisced yet.

The SEM observation on the floral organs of 'Serrano Chili' \((Capsicum annuum\ L.)\) and 'No. 178' \((Capsicum chinense\ Jacq.)\) showed a high similarity in epidermal morphology between these two pepper varieties which belong to two species. Therefore, the results will be presented here on the basis of each group of organs rather than each group of plants.
Sepals. At maturity, the sepals formed a five- or six-toothed campanulate calyx in both varieties. This calyx is green and persistent. In the SEM micrographs, the non-glandular hairs which are long, uniseriate, and multicellular, were present on the abaxial (external) surface (Fig. 15, 16, 19, 20); on the other side (Fig. 23, 24), the glandular hairs, which have a multi-celled head mounted on a one-celled stalk (two- or three-celled stalks were also found but very few), densely covered the whole adaxial (internal) surface. The epidermal cells around each non-glandular hair of the abaxial surface of 'Serrano Chili' were slightly raised and radiately arranged forming a multicellular hair-base (Fig. 15, 16).

Numerous small stomata were present on the abaxial (external) surface (Fig. 17, 21) but no stoma was found on the adaxial (internal) surface (Fig. 23, 24). The stomata on the sepals were superficial or slightly raised (Fig. 18; Fig. 22, at arrows).

The epidermal cells on both surfaces were irregularly shaped (Fig. 17, 21, 24); their outer walls were slightly convex. The cuticle of 'No.178' sepal epidermis (Fig. 21, 22) appeared smoother than that of 'Serrano Chili' (Fig. 17, 18) although both did not have obvious cuticle thickenings. The epidermal cells over the vascular bundles were forming some protuberances or ridges (Fig. 15, 19); between two ridges, the cells in the
uppermost region were horizontally elongated and these cells were evident on both abaxial (Fig. 20) and adaxial (Fig. 23) surfaces.

**P**etals. The corolla of 'No. 178' is greenish-white and that of 'Serrano Chili' is white. The petals fused at the flower base forming a corolla tube from which the free lobes arised.

A large amount of one-celled or two-celled hairs (trichomes) formed a "hair-zone" at each petal tip (Fig. 25, 29). The same type of hairs were produced continuously along the margins downwards to some region just above the fused corolla tube (Fig. 46). Hairs were not found in the other regions of a petal.

The epidermis of a petal is basically composed of hexagonal cells which have been slightly modified (Fig. 27, 28, 31, 32). On the adaxial surface, the epidermal cells in the costal regions (over the vascular bundles) were more or less elongated (Fig. 27) and the cells in the intercostal regions were more or less round-shaped (Fig. 32). On the abaxial surface, the epidermal cells in the costal region (Fig. 28) and the intercostal region (Fig. 31) were not differently shaped but the cells in the lower part of a petal showed more elongated shapes than those in the median and the upper parts. The outer walls of all epidermal cells were slightly domed (Fig. 27, 28, 31,
32); very weak cuticle thickenings crossing the cell walls were seen in some specimens (Fig. 27, 31) but not in other specimens (Fig. 28, 32).

Stomata were not found on the adaxial surface of a petal but were seen on the abaxial surface (Fig. 26, 30). For both varieties, the stomata were closely associated with the "hair-zone" of the petal tip (Fig. 26, 30). One stoma was found in the median part of the abaxial surface of one petal specimen (Fig. 31, at arrow); stomata have not been found in the lower part of a petal in all specimens examined.

Stamens. The position of the stamens is alternate with the petals. Each stamen consists of a tetrasporangiate anther (Fig. 33) and a filament (Fig. 45); the base of the filament attached to and fused with the "corolla tube" (Fig. 39, 43, 44, 46).

Hairs were not found anywhere on the anther and filament surface. In the SEM micrographs, the adaxial and the abaxial surfaces of a anther lobe were not different from each other in their appearance except that stomata were present and restricted in the region on the abaxial surface near the connective tissue (Fig. 35, at arrow; Fig. 37, 38). The epidermis of the anther lobes had slightly elongated hexagonal cells with the cell length oriented perpendicular to the long axis of the anther (Fig. 34, anther axis indicated by arrow). The outer walls of these cells were slightly domed and the cuticle was smooth (Fig.
The cells of the connective tissue were also slightly domed but irregularly shaped (Fig. 35, 38). The outermost surface of the partition between two locules in the same anther lobe appeared very smooth in the SEM micrographs (Fig. 36) and individual cells could not be detected. When a mature anther is dry, it dehisces longitudinally along this region.

The lower part of the filament merged into a "broadened base". This "base", together with its two lateral arm-like protuberances, attached to the lower part of the "corolla tube" (Fig. 39, 43, 44, 46). In the SEM micrographs, the epidermal cells of the filament were elongated with the long axis of the cell parallel to the filament length (Fig. 40, 41). The cuticle thickenings were parallel to the cell length and continuous from cell to cell (Fig. 40, 41). The outlines of these cells were marked longitudinally by wider cuticle ridges and horizontally by shallow depressions (Fig. 40, 41).

Stomata (Fig. 42) were found only on the adaxial surface of the filament; these stomata were restricted on the "broadened base" about the area where the lateral protuberances branched from (Fig. 47, at arrow; Fig. 48, partial enlargement of Fig. 47). The epidermal cells in this region were basically hexagonal but more or less modified (Fig. 42, 48). The cells above this region were elongated on the surface of the
protuberance and had cuticle thickenings (Fig. 47, 48, indicated by "2"). The epidermal cells in the upper region of the protuberance were not so elongated and had slightly domed outer walls (Fig. 47, 49, indicated by "3"); the cuticle thickenings were obvious in this upper region.

Carpels. In the early developmental stage of a pepper flower, two or three carpels (three are common) fuse into a syncarpous gynoecium. The upper part of this syncarpous gynoecium differentiates into a style and a stigma while the lower part develops into an ovary.

At maturity of a flower, a reticulate epidermal layer covered the stigmatic surface (Fig. 50). The cells of this epidermal layer had slightly domed outer walls; they were largely spaced and interconnected one another from different directions; they appeared sliding down into the center of the stigmatic surface (Fig. 56). The stigma of the pepper is considered to be the "wet type". Before the flower was open, the exudate began to be released through the intercellular spaces by the stigmatic surface; this could be detected by the bubble-like appearance of the epidermal cells and the wax contamination (Fig. 51). After the flower was fully open, the cuticle over the epidermis was ruptured (Fig. 52, 53) and more wax contamination was seen (Fig. 52).
In the center of the style was the transmitting tissue and its cells were elongated (Fig. 55). The cells of the transmitting tissue merged into the stigmatic tissue at one end and into the ovary wall at the other end (Fig. 56).

In the SEM micrographs, the epidermal cells of the external style surface were elongated with the long axis of the cell parallel to the style length (Fig. 54, 57); the cuticle thickenings were parallel to the cell length and continuous from cell to cell (Fig. 54, 57). In the 'Serrano Chili' specimens, the stoma was seen on the external surface of the style (Fig. 54) while in 'No. 178' style specimens, no stoma was found in this study.

The epidermal cells of the inner ovary wall were papillate (Fig. 59). The epidermal cells of the outer ovary wall, which were five- or six-sided, had slightly domed outer cell walls and their cuticle was smooth (Fig. 60). In the region around the ovary base, stomata were found for both 'Serrano Chili' (Fig. 61) and 'No. 178' (Fig. 62, 63).

Hairs were not seen on the surfaces of the gynoecium including the "stigma", "style" and "ovary". The hair seen in Fig. 62 is a "contamination".

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Discussion and Conclusions

Capsicum annuum L. and Capsicum chinense Jacq. are two closely related species, and this fact was reflected by the observation on the epidermal morphology of their leaves and floral organs in this study. The types of hairs, the types and distribution of stomata, and the configuration of epidermal cells for both leaves and flowers showed a high similarity between 'Serrano Chili' and 'No. 178'. This study also revealed some interesting morphological features about pepper leaves and flowers that are worth being discussed.

(1) Leaf epidermal morphology

Both adaxial and abaxial leaf surfaces of 'Serrano Chili' and 'No. 178' had one kind of glandular hair. This type of glandular hair has a multi-celled head mounted on a stalk. Gibson (1971, 1974) reported that the glandular hairs with a four-celled head mounted on a stalk were abundant on the wild potato plants but much less abundant on the cultivated potato plants. Gibson found that this four-celled gland will release an exudate when damaged, and the exudate can cause the insects (e.g., aphids) to stick on the plant surface and restrict their movement.

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The function of the glandular hairs found on pepper leaves can not be predicted in this study. These hairs were seen scattered in the intercostal regions of both leaf surfaces; these hairs appeared closely associated with the small veins (Fig. 9).

The non-glandular hairs of 'No. 178' were shorter than those of 'Serrano Chili'. The elongated non-glandular hairs in 'No. 178' were composed of different sized or shaped cells, and showed a tendency to branch (Fig. 8, 11). Some glandular hairs and non-glandular hairs had an enlarged basal cell surrounded by radiately arranged epidermal cells (Fig. 10). The latter non-glandular hairs were shorter and had a conical appearance. Whether these short non-glandular hairs on the 'No. 178' leaf surface are representatives of another hair type or they are just the immature long hairs can not be concluded here. Some elongated hairs on the apical margins of 'Serrano Chili' also had an enlarged basal cell (Fig. 6), but the component cells apparently had equal diameter.

F1 plants of "Serrano Chili X No. 178" showed a typical leaf appearance of 'Serrano Chili' when they are looked at by the naked eye. The interesting thing is that, under SEM observations, the non-glandular hairs of F1 skewed to the 'No. 178' parent type (Figs. 12-14). A possible situation can be suggested by this morphological study: the 'No. 178' parent
contributed the "hair-type" while the 'Serrano Chili' parent contributed the "abundance" and the "elongation" of leaf hairs to their progeny in the F1 generation.

(II) Epidermal morphology of floral organs

Sepals. The slightly raised stomata were found on the abaxial side (external surface) of pepper sepals in this study. Raised stomata were found on the Coleus stems (Turner and Lersten, 1983), tomato sepals (Chandra Sekhar, 1984), and some seedling roots (Christodoulakis and Psaras, 1987; Tarkowska and Wacowska, 1988). No environmental influences were related to these raised stomata; Turner and Lersten (1983) suggested that this is a genetically determined feature.

The pepper calyx has a very uneven surface. The raised stomata on the abaxial surface of the pepper sepals may be caused by the "physical nature of the surface" of the sepal epidermis. This explanation is possible because not all the stomata were raised and some hairs on the sepal abaxial surface had a slightly raised base, too. In addition, the major stomatal type appeared anisocytic and was consistent with that of pepper leaves.
Petals.  Short hairs were present at the tip and the margins of each pepper petal. The function of these hairs is considered to hold the adjacent petals together. It is interesting to find that stomata were present only on the abaxial surface of a petal and were closely associated with the "tip-hair-zone".

The stomata on the seedling roots were reported being associated with the "root-hair-zone" and having the root hairs as the subsidiary cells (Lefebvre, 1985; Christodoulakis and Psaras, 1987; Tankowska and Wacowska, 1988). It was suggested that the stomata in the root-hair-zone function as part of the root aeration system although they might not have normal stomatal function.

Whether the hairs on the pepper petals have other functions is still unknown; therefore, the most possible explanation for the association of stomata with hairs seems "aeration", the similar role as the stomata in the root-hair-zone play.

Stamens.  The epidermal cells on pepper anthers were slightly elongated and oriented with the long axis of the cell more or less at the right angles to the axis of the anther. The cuticle over the epidermis was smooth and thickenings were
not seen at all. This appearance is quite different from the surface features observed on the anthers of Zea Mays (Cheng, et. al., 1979), Lycopersicon esculentum (Chandra Sekhar and Sawhney, 1984), and Brassica napus (Polowick and Sawhney, 1986). The anthers of these plant species all have the long axis of their epidermal cells parallel to the axis of the anther and obvious cuticle thickenings.

Cheng et al. (1979) assumed that the development of cuticle thickenings probably forms a rigid anther-wall which gives the additional force to accomplish the anther dehiscence. If this is true, the smooth cuticle will be a weak point for anther dehiscence. The arrangement of epidermal cells with the cell length perpendicular to the anther length is probably the design for overcoming the weakness of the smooth cuticle.

The stomata were found only on the abaxial surface of the anther and restricted in the area near the connective tissue (Fig. 35, 37, 38). This situation is similar to that in Brassica (Polowick and Sawhney, 1986). The connective tissue is the place where the vascular bundle passes in the anther, but whether the stomata and the vascular bundle have some relationship is difficult to predict. Before anther dehiscence, anthers enclose the ovary and part of the style
(in some varieties, they enclose whole gynoecium) with their abaxial surfaces exposed to the environment; water loss may be increased through these stomata. The faster local dehydration in this area, together with the horizontally arranged epidermal cells, may give a pulling force for anther dehiscence.

The lower part of each filament merged into a "broadened" base which together with its two "protuberances", attached to the corolla tube. Stomata were seen only on the adaxial surface and were restricted on the "broadened base" of each filament. On the adaxial view of the petal, the space between these two "protuberances" formed the groove mentioned by Martin, et al. (1932).

According to Martin, et al., these grooves on the corolla tube and the duck-like spaces between the backs of the filaments and the corolla tube are the places for secreting and conducting nectar. The stomata found only on the "broadened base" may have showed another piece of evidence for that the epidermal cells or the subepidermal cells of this "broadened" filament base are serving as nectaries. The nectar may be released through the stomata associated with these nectaries and flow into the "grooves" or "duct-like spaces". That the stomata associated with the nectary is not uncommon, e.g., in Brassica napus, the stomata are also related to nectaries (Polowick and Sawhney, 1986).
Carpels. The stigmatic surface of *Capsicum* examined in this study is different from the stigmatic surfaces of *Petunia* (Konar and Linskens, 1966), *Lycopersicon* (Dumas, et al., 1978; Kadej, et al., 1985), and *Nicotiana* (Cresti, et al., 1986; Kandasamy and Kristen, 1987). In the latter genera, the stigmatic epidermis differentiates into one- or two-celled papillae while in *Capsicum*, the stigmatic surface is one net-like cell layer with the component cells having just slightly domed outer walls.

Cochran and Dempsey (1966) reported that the stigma of the pimiento pepper (*Capsicum*) flowers was papillate and covered with a viscous fluid. These authors studied the stigma at the flowering stage and they didn't observe the stigma with a SEM; therefore, the papillae they mentioned were probably just the cuticle of epidermal cells pushed outward by the exudate accumulation under it (Fig. 51, 53).

Stomata were found on the epidermis of the style in 'Serrano Chili' but not on the stylar epidermis of 'No. 178'. Stomata were also found on the stylar surfaces of *Lycopersicon esculentum* (Chandra Sekhar and Sawhney, 1984), *Lycopersicon peruvianum* (Webb and Williams, 1988), or *Brassica napus* (Polowick and Sawhney, 1986). The function of these stomata on the surface of a style is unknown. The green
chloroplasts have been found in the transmitting cells of both *Nicotiana* (Bell and Hicks, 1976) and *Lycopersicon* (Webb and Williams, 1988). Although these authors suggested a photosynthetic activity, Bell and Hicks didn't mention if the stomata were present on the styles in their material, and Webb and Williams didn't conclude the relationship between the chloroplasts in the transmitting cells and the stomata on the stylar surface.

The stomata on the ovary base of a pepper flower represent another interesting observation in this study. The stomata were found only on the basal part of the ovary for both 'Serrano Chili' and 'No. 178'.

Hunting (1974) have found that two distinctive zones occurred on a mature ovary wall or the pericarp of a young fruit in *Capsicum annuum* L., and the lower part of the ovary wall remained meristematic. He also found that a developing pepper fruit grew most strongly at the base. Huber (1980) reported that the nectaries of most Solonaceae species he examined were on the base of the gynoecium; in the genus *Capsicum*, a ring-shaped nectary gland was found to differentiate at the ovary base, although Martin, et al. (1932) did not find any indication that the ovary of the genus *Capsicum* functions as a nectary.
On the epidermis of the outer ovary wall, because the stomata were found only on its very lower part, two possible explanations can be given here. One is that the ovary base serves as the nectary gland which was suggested by Huber (1980) and supported by the fact that most species in Solanaceae have their nectaries on the ovary base. The other is that the stomata may have normal stomatal function because the ovary base is meristematic (Munting, 1974) and therefore, the rate of respiration may be high.
Fig. 1-4. Leaf epidermis of 'Serrano Chili' pepper (Capsicum annum L.). Scale bar = 500 μm in Fig. 1, 2, and = 50 μm in Fig. 3, 4. (1) Abundant hairs on the adaxial surface. (2) Less abundant hairs on the abaxial surface; the glandular hairs scattering in the intercostal region. (3) Epidermal cells of the adaxial surface showing sinuous cell outlines, slightly domed outer walls, and one stoma. (4) Epidermal cells of the abaxial surface showing the similar appearance as that of the adaxial surface.
Fig. 5, 6. Hairs on the margins of the 'Serrano Chili' leaf; pictures taken from the adaxial side. Scale bar = 50 \mu m. (5) Hairs on the margin of the median part of a leaf. (6) Hairs on the margin of the apical part of a leaf. Note the enlarged basal cell (at arrows). Fig. 7. Regular hair-base for both glandular and non-glandular hairs on the adaxial leaf surface of 'Serrano Chili'. Scale bar = 50 \mu m.
Fig. 8-11. Leaf epidermis of 'No. 178' pepper (Capsicum chinense Jacq.). Scale bar = 500 um in Fig. 8, 9, and = 50 um in Fig. 10, 11. (8) The adaxial surface showing elongated, non-glandular hairs concentrated on the large vein. (9) The abaxial surface showing the elongated, non-glandular hairs on the large veins, and the glandular hairs being associated with the small veins (at arrows). (10) Hair-base for both glandular and non-glandular hairs on the adaxial leaf surface. Note the enlarged basal cells (at arrows). (11) Elongated non-glandular hairs showing branching (at arrows).
Fig. 12-14. Leaf epidermis of F1 plants of "Serrano Chili X No. 178". Scale bar = 500 um in Fig. 12, 14, and = 50 um in Fig. 13. (12) Hairs on the adaxial surface of the F1 leaf. Note the "hair-base" of short hairs (at arrows). (13) The enlarged cell-base indicated by arrows in Fig. 12. Note the basal cell and the radiately surrounded epidermal cells. (14) Hairs on the abaxial surface of the F1 leaf. Note the enlarged hair-base (at arrows).
Fig. 15-18. The epidermal morphology of the abaxial surface of 'Serrano Chili' sepal. Scale bar = 500 μm in Fig. 15, = 50 μm in Fig. 16-18. (15) The epidermis over the vascular bundle forming a "ridge" of the sepal. (16) The multi-celled base of two elongated hairs framed by the square of Fig. 15. (17) Numerous stomata are present on the abaxial sepal surface. (18) The slightly raised stomata sometimes found on the abaxial sepal surface.
Fig. 19-22. The epidermal morphology of the abaxial surface of 'No. 178' sepal. Scale bar = 500 μm in Fig. 19, and = 50 μm in Fig. 20-22. (19) The epidermis of the abaxial sepal surface showing a "short ridge" occurring between two "long ridges". (20) The area framed by the square in Fig. 19, showing the horizontally elongated cells between ridges. (21) Numerous stomata are present on the abaxial sepal surface. (22) Slightly raised stomata (at arrow) and slightly domed outer cell walls.
Fig. 23, 24. The epidermal morphology of the adaxial surface of 'Serrano Chili' sepal. Scale bar = 50 μm. (23) The adaxial surface of the region between two sepal ridges. (24) The glandular hairs densely covering the adaxial surface of sepals.
Fig. 25, 26. The epidermal morphology of a 'Serrano Chili' petal. Scale bar = 50 um. (25) Numerous short hairs at the tip of a petal. Ab, abaxial surface; Ad, adaxial surface. (26) Stomata in the area slightly below the "tip-hair-zone" on the abaxial surface of a petal. Note the stomata closely associated with the hairs.
Fig. 27, 28. The epidermal morphology of a 'Serrano Chili' petal. Scale bar = 50 μm. (27) Adaxial surface of a petal; the epidermal cells over the vascular bundle are slightly elongated. V, vascular bundle. (28) Abaxial surface of a petal; the vascular bundle do not show elongated epidermal cells. V, vascular bundle.
Fig. 29-32. The epidermal morphology of a 'No. 178' petal. Scale bar = 50 um. (29) Short hairs are numerous at the tip. (30) The stomata on the abaxial petal surface. Note these stomata closely associated with the tip-hair-zone. (31) The epidermal cells in the intercostal region of the abaxial surface. A stoma was found in this specimen (at arrow). Ab, abaxial surface. (32) The epidermal cells in the intercostal region of the adaxial surface. Ad, adaxial surface.

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Fig. 33. A cross section from the mature 'No. 178' flower bud. The anther of pepper flowers is tetrasporangiate; in this bud, the partition between two locules in each anther lobe was broken already. a, abaxial side of an anther lobe; c, connective tissue between two lobes; d, the region where the dehiscence occurs. X 40. Fig. 34-36. The epidermal morphology of the pepper anther. Fig. 34, 35. Specimen from 'Serrano Chili' anther. Scale bar = 50 um. Fig. 36. Specimen from 'No. 178' anther. Scale bar = 5 um. (34) Abaxial surface of an anther lobe, the anther axis indicated by "arrow". Note the arrangement of epidermal cells at right angle to the anther axis. (35) The surface of the connective tissue on the abaxial side of the anther. Note the stoma on the near lobe surface (at arrow). (36) Very smooth cuticle over the region for dehiscence.
Fig. 37, 38. Stomata on the abaxial surface of an anther lobe near the connective tissue. (37) Specimen from 'Serrano Chili'. Scale bar = 50 um. (38) Specimen from 'No. 178'. Scale bar = 5 um.
Fig. 39-42. Epidermal morphology of the 'No. 178' filament.

Scale bar = 50 μm in Fig. 39, and = 5 μm in Fig. 40, 41, 42.

(39) The "broadened base" of a filament, together with its arm-like protuberance, attached to the corolla tube. Ad, adaxial surface; dc, duck-like space between the petal and the filament back; g, groove formed by two adjacent protuberances. (40) Adaxial surface of a filament showing elongated ells and obvious cuticle thickening. (41) Abaxial surface of a filament showing elongated cells and wider cuticle thickenings. (42) A stoma found on the adaxial surface of the filament base.
Fig. 43-45. Cross sections of mature 'No. 178' buds showing the possible area for nectar secreting. (43) A cross section showing the relationship of petal and filament at the lower part of a flower bud. P, petal; Fi, filament; dc, duck-like space; g, groove; O, ovary. X 40. (44) A cross section at the level slightly higher than that of Fig. 43. S, sepal; P, petal; Fi, filament; dc, duct-like space; g, groove; O, ovary. X 40. (45) A cross section at the level slightly higher than that of Fig. 44. S, sepal; P, petal; Fi, filament; g, groove. X 40.
Fig. 46. Two adjacent petals with two filament bases attached to and fused with the "corolla tube area". Specimen from 'Serrano Chili'. P, petal; Fi, filament; g, groove. Scale bar = 500 um.
Fig. 47-49. The epidermal morphology of the "broadened base" of a 'Serrano Chili' filament. Scale bar = 50 um in Fig. 47, 48, and = 5 um in Fig. 49. (47) "Broadened base" of a filament with its arm-like protuberance. Note the stomata scattering only on the surface of its lower part (at arrows). Region 1-3 are enlarged in Fig. 48, 49. (48) Region 1 and 2 of Fig. 47. Note the different cell shapes between Region 1 and 2. (49) Region 3 of Fig. 47. Note the cell shape and cuticle thickenings.
Fig. 50-53. Stigma surface of 'Serrano Chili'. Scale bar = 50 μm in Fig. 50, 51, 52, and = 5 μm in Fig. 53. (50) A net-like epidermal layer covering the mature stigma surface; three depressions indicating three carpels fusing this gynoecium. (51) and (52) Stigma surface before flower opening. Note the domed shaped cell and the contamination by their exudate. (53) Stigma surface after flower opening. Note the ruptured cuticle.
Fig. 54. Outer epidermal surface of the 'Serrano Chili' style showing a stoma lying between cuticle thickenings. Scale bar = 5 um. Fig. 55. Elongated cells of the transmitting tissue of 'Serrano Chili'. TT, transmitting tissue. Scale bar = 50 um.
Fig. 56. Internal view of a 'No. 178' style. Scale bar = 500 um. Fig. 57. External surface of a 'No. 178' style showing the elongated cells and cuticle thickenings. Scale bar = 5 um. Fig. 58, 59. Internal view of a 'No. 178' ovary. Scale bar = 500 um in Fig. 58, and = 50 um in Fig. 59. (58) Ovules borne on the placental tissue. (59) Papillate epidermal cells of the inner ovary wall (the region framed by the square of Fig. 58).
Fig. 60, 61. Epidermal surface of outer ovary wall of 'Serrano Chili'. Scale bar = 5 um. Fig. 62, 63. Epidermal surface of outer ovary wall of 'No. 178'. Scale bar = 50 um in Fig. 62, and = 5 um in Fig. 63. (60) The epidermis showing its basical five- or six-sided cells and slightly domed outer walls. (61) The stoma on the ovary base. (62) Stomata scattering on the surface of the ovary base. The hair in this picture was a contamination; no hair was found on the ovary. (63) The stoma on the ovary base at higher magnification.
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Dai-Mei Shuh was born in Taipei, Taiwan, R.O.C., on March 11, 1953, the first child of I-Shun Lu and Chun-Ta Shuh. She grew up with her grandparents and accepted her education in the elementary and secondary schools in her home city, Taipei. She received her Bachelor of Science degree in Horticulture in National Chung-Hsing University, Taichung campus, in 1976. After her college education, she has been a garden manager and a teacher of the vocational high school.

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DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: Dai-Mei Shuh

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Title of Dissertation: GENETICS AND MORPHOLOGY ASSOCIATED WITH THE FLOWERING PATTERN, FLOWERS, AND LEAVES OF Capsicum annuum L. AND Capsicum chinense Jacq.

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