4. Bunemann, G. and A. Struklec. 1980. Effect of summer pruning treatments of vigorous apple trees on the nutrient contents of foliage and fruits, p. 216–217. In: D. Atkinson, J.E. Jackson, R.O. Sharples, and W.M. Waller (eds.). Mineral nutrition of fruit trees. Butterworths, London.
5. Elfving D.C. and C.G. Forshey. 1976. Growth and fruiting responses of vigorous apple branches to pruning and branch orientation treatments. J. Amer. Soc. Hort. Sci. 101:290–293.
6. Gardner, V.R., F.C. Bradford, and H.D. Hooker, Jr. 1939. The fundamentals of fruit production, 2nd ed. McGraw-Hill, New York. p. 489–507.
7. Greene, D.W. and W.J. Lord. 1978. Evaluation of scoring, limb spreading and growth regulators for increasing flower bud initiation and fruit set on young 'Delicious' apple trees. J. Amer. Soc. Hort. Sci. 103:208–210.
8. Hansen, P. 1967. ^{14}C studies on apple trees III. The influence of season on storage and mobilizatin of labelled compounds. Physiol. Plant. 20:1103–1111.
9. Lakso, A.N. and S.G. Carpenter. 1978. Control of regrowth in mechanically-hedged apple trees with NAA and daminozide. HortScience 13:55–56.
10. Lord, W.J. and D.W. Greene. 1982. Effects of summer pruning on the quality of 'McIntosh' apples. HortScience 17:372–373.
11. Lord, W.J., D.W. Greene, and R.A. Damon, Jr. 1975. Evaluation of fruit abscission and flower bud promotion capabilities of ethephon and SADH on apples. J. Amer. Soc. Hort. Sci. 100:259–261.
12. Lord, W.J., D.W. Greene, W.J. Bramlage, and M. Drake. 1979. Inducing flowering of apple trees and increasing fruit quality by summer pruning. Compact Fruit Tree 12:23–29.
13. Marini, R.P. and J.A. Barden. 1982. Growth and flowering of vigorous apple trees as affected by summer or dormant pruning. J. Amer. Soc. Hort. Sci. 107:34–39.
14. Marini, R.P. and J.A. Barden. 1982. Yield, fruit size, and quality of three apple cultivars as influenced by summer or dormant pruning. J. Amer. Soc. Hort. Sci. 107:474–479.
15. Marini, R.P. and J.A. Barden. 1982. Effects of summer vs. dormant pruning and NAA treatment on growth of one-and two-year-old apple trees. J. Amer. Soc. Hort. Sci. 107:604–607.
16. Pearson, A.H. 1895. Pruning fruit trees. J. Royal Hort. Soc. 19:270–279.
17. Perring, M.A. and A.P. Preston. 1974. The effect of orchard factors on the chemical composition of apples. III. Some effects of pruning and nitrogen application on Cox's Orange Pippin fruit. J. Hort. Sci. 49:85–93.
18. Preston, A.P. and M.A. Perring. 1974. The effect of summer pruning and nitrogen on growth, cropping and storage quality of Cox's Orange Pippin apples. J. Hort. Sci. 49:77–83.
19. Taylor, B.H. and D.C. Ferree. 1981. The influence of summer pruning on photosynthesis, transpiration, leaf abscission, and dry weight accumulation of young apple trees. J. Amer. Soc. Hort. Sci. 106:389–393.
20. Terblanche, R.D. and W.J. Pienaar. 1977. The effect of pruning practice on the intensity of bitter pit in Cox's Orange Pippin. Decid. Fruit Grow. 27:66–70.
21. Toenjes, W. 1949. The effect of trunk girdling on inducing earlier bearing of Northern Spy apple trees. Mich. Agr. Expt. Sta. Quart. Bul. 32:23–27.
22. Utermark, H. 1977. Summer pruning to control growth and maintain fruiting in mature apple trees. Compact Fruit Tree 10:86–90.
23. Veinbrants, N. 1972. Effects of succinic acid-2,2-dimethylhydrazide (Alar) or scoring on growth and flower initiation of young apple trees. Austral. J. Expt. Agr. Animal Husb. 12(54):89–95.
24. Vincent, C.C. 1917. Winter versus summer pruning of apple trees. Ida. Agr. Expt. Sta. Bul. 98.
25. Weis, S.A., M. Drake, W.J. Bramlage, and J.H. Baker. 1980. A sensitive method for measuring changes in calcium concentration in 'McIntosh' apples demonstrated in determining effects of foliar calcium sprays. J. Amer. Soc. Hort. Sci. 105:346–349.
26. Williams, M.W. 1972. Induction of spur and flower bud formation in young apple trees with chemical growth retardants. J. Amer. Soc. Hort. Sci. 97:210–212.

J. Amer. Soc. Hort. Sci. 108(4):595–600. 1983.

Inflorescence and Floral Development in *Pelargonium* X *hortorum*

Hazel Y. Wetzstein and Allan Armitage
Department of Horticulture, University of Georgia, Athens, GA 30602

Additional index words. hybrid geranium, flower initiation

Abstract. **Floral initiation and development in the hybrid geranium, *Pelargonium* X *hortorum* Bailey, were examined using scanning electron microscopy. Inflorescence initiation was marked by a raising of the apex followed by the formation of convex flower primordia. In floral development, 5 sepal primordia were delimited, closely followed by 5 petal primordia. Imbricate sepals enclosed the floral apex during later developmental stages. Five antesepalous, then 5 antepetalous stamen primordia were initiated. Five gynoecial primordia arose, forming a pentagonal ridge, carpellary lobes, and eventually an elongate style with stigma. Three of the antepetalous stamen primordia developed into filaform staminodia.**

The floral ontogeny of members of the Geraniaceae has been described (2, 3, 5, 7, 8) by light microscopic observations and line drawings or photographs. Miranda and Carlson (4) described early initiation and the finally differentiated inflorscence in the hybrid geranium; however, they did not show intermediate changes. It appears that there has not been a complete description of floral initiation and organogenesis of the hybrid geranium. This study describes the floral initiation and sequential development of the hybrid geranium using scanning electron microscopy (SEM).

Received for publication July 6, 1982. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

Materials and Methods

Hybrid geranium seeds, 'Sprinter Scarlet', were germinated under intermittent mist and grow in 10-cm pots in sphagnum peatmoss–vermiculite media amended with superphosphate and minor nutrients. Plants were fertilized at each irrigation with 200 ppm N using 15N–0P–12.5K. Every 4th irrigation was with

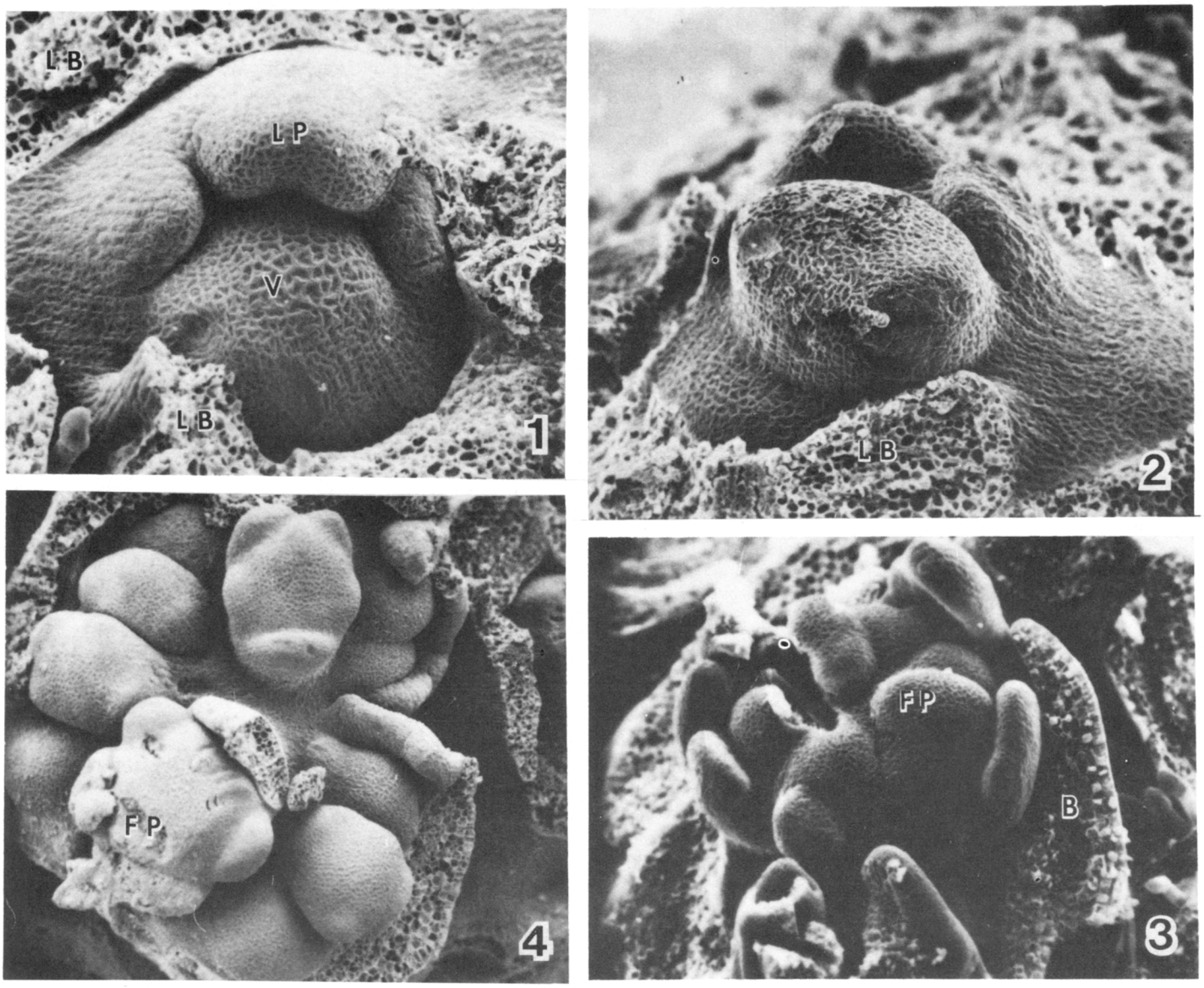


Fig. 1–4. Development of inflorescence from the vegetative state.—**1.** Slightly convex vegetative apical meristem with leaf primordium and vegetative apex surrounded by leaf bases of removed leaves. ×200. **2.** Enlarged and raised apical meristem. ×200. **3.** Numerous, convex floral primorida. ×200. **4.** Inflorescence with distinct floral initials, some showing early stages of sepal development. ×100—B = bract, FP = floral primordium, LP = leaf primordium, LB = leaf base, V = vegetative meristem.

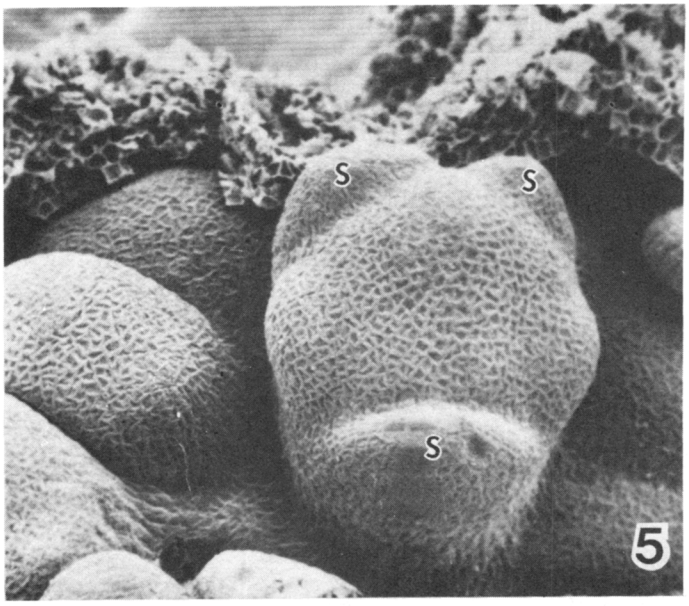
tap water only to minimize soluble salt accumulation. Night temperature was 16 ± 3°C; day temperatures fluctuated with ambient temperature but were never below 21°. Terminal apices from 4 plants were collected every week and prepared for SEM. Buds were dissected to suitable size for processing using a stereo light microscope.

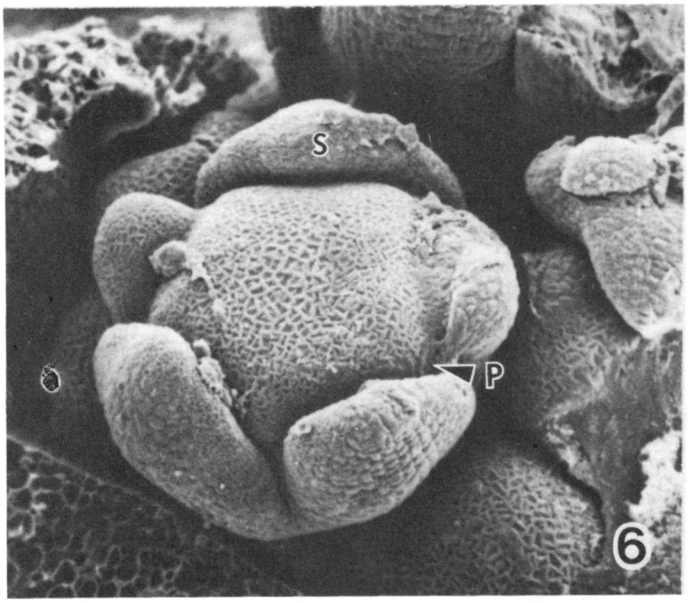
Tissues were fixed in 2% glutaraldehyde in 0.1M cacodylate buffer, pH 7.2, serially dehydrated in ethanol and critical-point–dried with CO_2. Apices were mounted on aluminium stubs and dissected selectively to expose desired organs or structures. Tissues were sputter-coated with gold–palladium and observed with a Cambridge Mark IIA SEM.

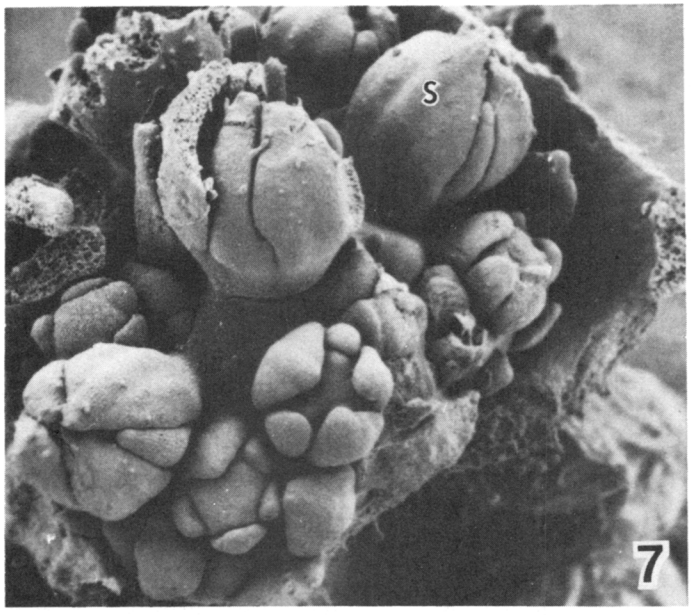
Results

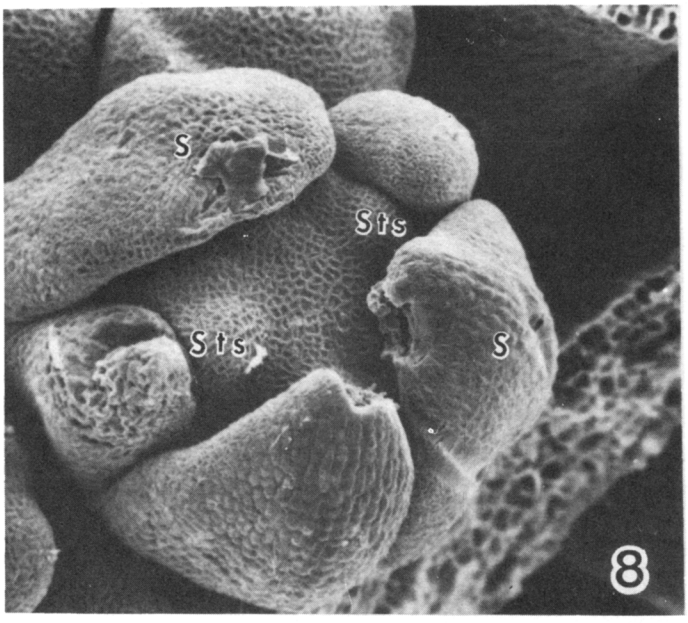
The flower in *Pelargonium* X *hortorum* is perfect, complete, and 5-merous with 5 sepals, 5 petals, and 10 stamens. The flowers are borne in an umbelliform dichasium.

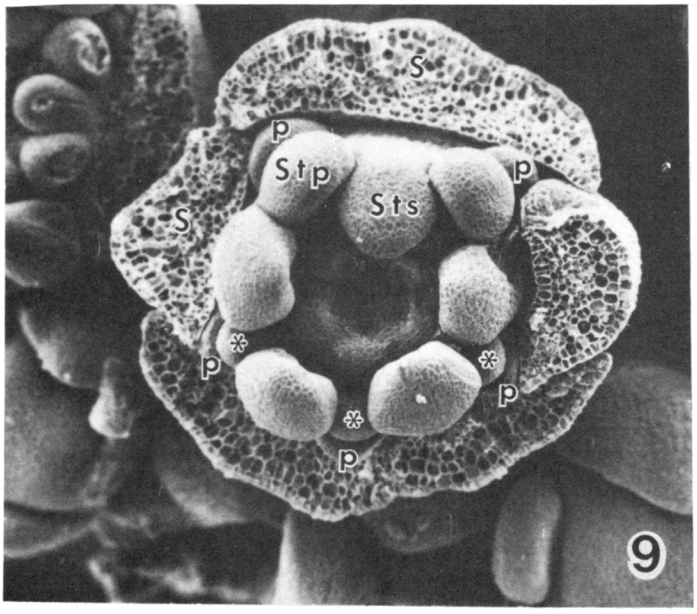
Fig. 5–10. Development of the flower.—**5.** Initiation of first 3 sepal primordia. ×200. **6.** Further development of additional sepals with petal initiation. ×200. **7.** Inflorescence with individual floral initials in varying stages of development. Imbricate nature of sepals are evident. × 50. **8.** Floral bud with enlarged sepals and protuberances of antesepalous stamen primordia. ×200. **9.** Further differentiated flower, top view. Sepals have been removed to expose developing androecium and gynoecium. Petal primordia remain small. Antesepalous and antepetalous stamen primordia are distinct. Three smaller antepetalous stamen primordia will develop into sterile stamenoidia. ×200. **10.** Lateral view of developing flower from which sepals have been removed showing relative position and small size of petal primordia. Gynoecial primordia are visible. One antepetalous stamen primordium and some petal primordia are hidden from view. ×200.—S = sepal, P = petal, Stp = antepetalous stamen primordium, Sts = antesepalous stamen primordium, asterisk = sterile staminoidium primordium.

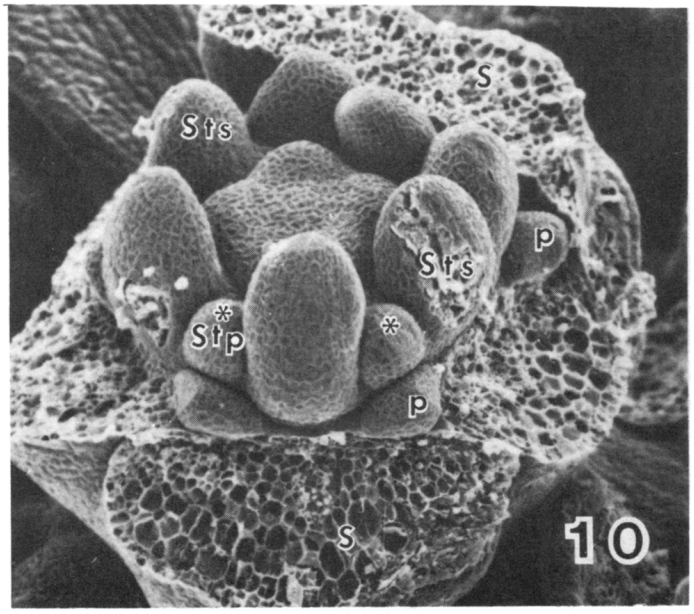












Inflorescence initiation and development. The vegetative apical meristem is a slightly convex (Fig. 1). Leaf primordia are initiated singly, high on the sides of the apex (Fig. 1). In the initiation of the inflorescence apex there is an increase in height and constriction of the apex (Fig. 2), followed by formation of flower primordia (Fig. 3). The inflorescence broadens considerably and increases in height (Fig. 3). In older inflorescences (Fig. 4), distinct floral initials are apparent at different stages of development. Generally, one or 2 flower primordia are at a further-developed stage than other flowers within the same infloresence (Fig. 4).

Floral differentiation. The stages of floral development are chronologically listed in Table 1. During the development of a single floral primordium, sepal primordia are initiated (Fig. 5). The first and 2nd sepal primordia form, with the 3rd forming in close proximity to the 2nd. The 4th and 5th sepal primordia then successively initiate adjacent to the first (Fig. 6). Petal primordia are initiated; however, development is restricted and they persist as 5 rounded projections for some time, enfolded between the sepals and stamens. A given inflorescence has floral initials with sepals in varying stages of development (Fig. 7). Sepals are imbricate and closely enclose the developing floral apex. The calyx remains regular until the time of pistil development. An indentation develops between the areas of the sepal and receptacle forming an elongate calyx spur. Antesepalous stamen primordia are initiated as rounded mounds (Fig. 8) and are then followed by the slightly centrifugal development of 5 antepetalous stamen primorida (Fig. 9). Five antesepalous and 5 antepetalous stamen primordia are present. Three of the antepetalous stamen primordia are somewhat smaller (Fig. 9); these smaller stamen primordia will develop into sterile filamentous staminodia. The larger antepetalous stamen primordia and all antesepalous stamen primordia will develop fertile stamens. At this stage the petals are small and positioned between and interior to the sepals (Fig. 10). Five gynoecial primordia are visible (Fig. 10). Raised pentagonal ridges form during carpel development (Fig. 11), followed by the gynoecium increasing in height and forming a central locular depression and carpellary lobes (Fig. 12). The petals expand and flatten and will form a laminate, petaloid corolla (Fig. 12). Stamens develop filaments and anther lobes; 3 antepetalous stamenoidia (2 visible) have elongated (Fig. 12). The androecium thus consists of 5 antesepalous stamens alternating with 2 antepetalous stamens and 3 antepetalous staminodia. Further development of the gynoecium involves elongation of the style column and differentiation of ovary, style, and stigma (Fig. 13). Styles are adnate to the elongate axis (Fig. 13). Present on the gynoecium are numerous epidermal hairs (Fig. 14); filaments and staminodia are elongated (Fig. 13, 14). Separation and coiling of the styles expose a papillate stigmatic area (Fig. 15). Abundant uniseriate-covering hairs and glandular trichomes are present covering the entire gynoecium (Fig. 16).

Table 1. Sequence of inflorescence and floral development in *Pelargonium* X *hortorum*.

Developmental sequence		Fig. in text
Inflorescence development		
Stage	Event	
0	Vegetative apex	1
1	Dome formation	2
2	Initiation of floral initials	3
3	Floral developmental stages visible	4
Floral development		
Stage	Event	
1	Sepal primordia	5, 6
2	Petal primordia	6
3	Sepal enlargement	8
4	Antesepalous stamen primordia	8
5	Antepetalous stamen primordia	9, 10
6	Differentiation of stamen primordia; Pentagonal ridge of gynoecium	9, 10
7	Stamens with differentiated anther and filament; 3 Antepetalous stamen primordia forming staminodia; Carpellary lobes, central locular depression	12
8	Elongation of style column, pubescence on gynoecium	13, 14
9	Separation and coiling of styles, papillate stigmatic area	15

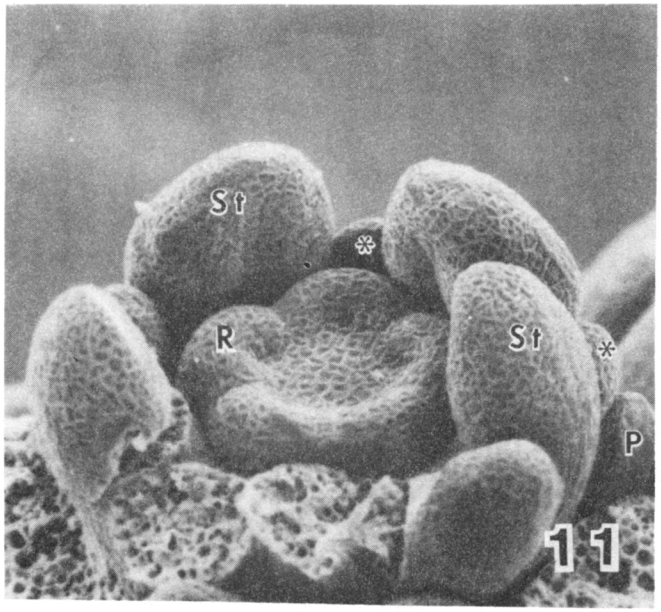
Discussion

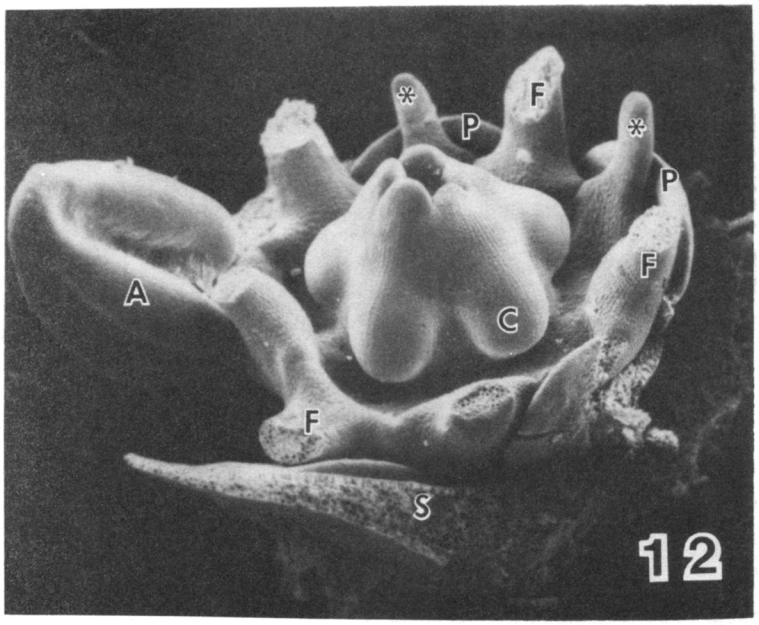
The inflorescence of *Pelargonium* has been described as an umbel (1, 6). However, it meets this criterion only in terms of its general form; i.e., as an inflorescence composed of several branches that radiate from almost the same point on a common peduncle. The *Pelargonium* inflorescence lacks the centripetal, indeterminate characteristics of the umbel and can be referred to more correctly as an umbelliform dichasium (9) or as a series of dichasia (10). The inflorescences of several members of the Geraniaceae are discussed by Zanker (10).

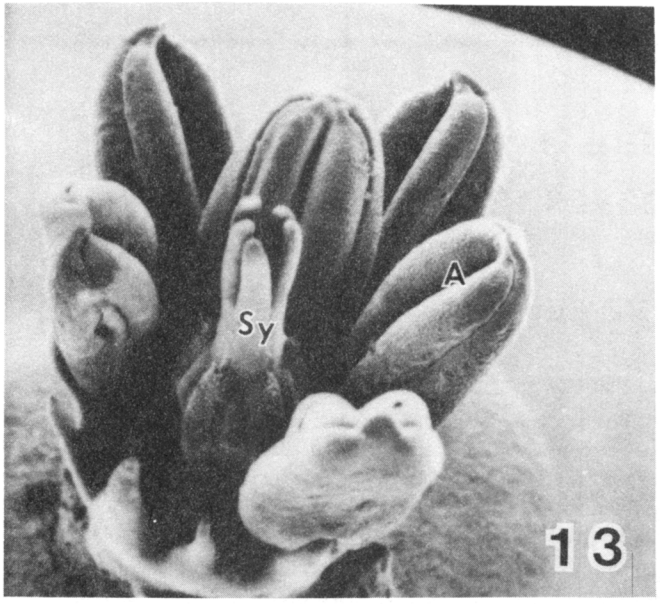
Payer (5) describes 4 genera in the order Geraniales: *Geranium, Erodium, Pelargonium*, and *Monsonia*. Floral characteristics of the group are discussed, as are specific attributes for each genus. His descriptions of *Pelargonium inquinans* differ somewhat from that seen in *P.* X *hortorum* in the order of sepal initiation. His descriptions of corolla initiation are similar, however, and androecium development is much the same with 2 stamen whorls and a similar reduction of 3 antepetalous stamens to filaments without anthers.

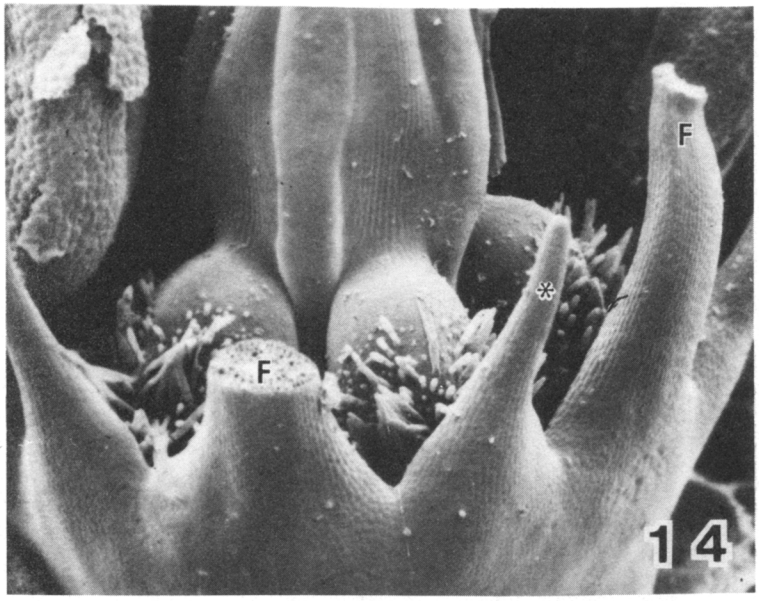
Sattler (7) describes the floral organogenesis of *Pelargonium zonale*. The initiation of the antepetalous stamens appears to occur centrifugally at a level more distinctly different from the antesepalous stamens and petal primordia than in *P* X *hortorum*. Otherwise, Sattler's description concurs with the developmental pattern observed in *P.* X *hortorum*. Obdiplostemony represents an interruption in the usual sequence of alternation in floral whorls; thus, its morphological nature has been of interest. The

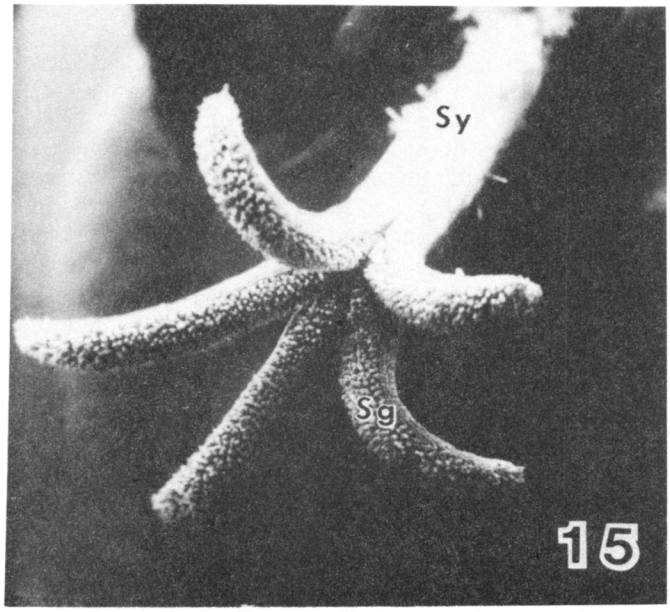
Fig. 11–16. Flower development.—**11.** Flower with sepals and 2 stamen primordia removed to illustrate gynoecial development and pentagonal ridge formation during carpel development. Two staminodia and a petal are visible. ×200. **12.** Flower with sepals and all but one anther removed. Gynoecium with distinct carpellary lobes and central locular depression. Stamens have developed filaments and anther lobes. Filament bases alternate with sterile staminodia. Petals have expanded and flattened. ×50. **13.** Flower with sepals, petals, and one anther removed. Enlargment and growth of style column is evident; styles are elongate and adnate. ×20. **14.** Elongated filaments and staminodia are visible. Note numerous epidermal hairs on gynoecium. ×50. **15.** Separation and coiling of styles exposing papillate stigmatic area. ×20. **16.** Glandular hairs on ovary. ×200.—A = anther, C = carpellary lobes, F = filament, P = petal, R = pentagonal ridge, S = sepal, St = stamen primordium, Sg = stigmatic area, Sy = style, asterisk = staminodia.

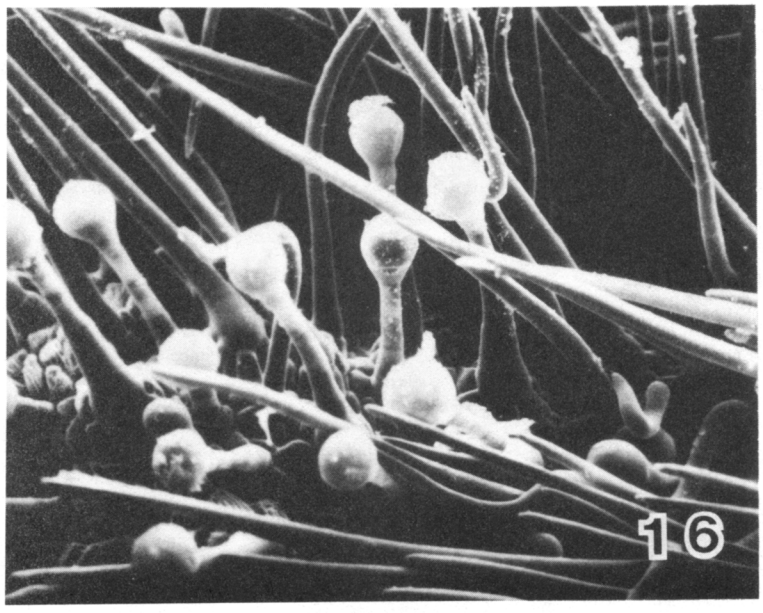












obdiplostemony of members of the Geraniaceae has been studied by Eckert (2) in regard to organogenesis, histogenesis, and vascularization. In *Geranium nodosum*, antesepalous stamen initiation precedes antepetalous stamen initiation, with the primordia standing in one whorl. Obdiplostemony is derived from "displacement" or increased growth of episepalous areas.

The flowers of *Pelargonium* are irregular, differing from other members in the Geraniaceae with the development of a calyx with a spur united to the pedicel. Sauer (8) describes some of the later developmental stages and mature flower of *Pelargonium zonale* with a discussion of spur formation. Labbe (3) describes spur development in three species: *P. endlicheranum*, *P. peltatum*, and *P. zonale*. Similar development occurs in *P.* X *hortorum*.

Literature Cited

1. Bailey Hortorium. 1976. Hortus third. MacMillan, New York.
2. Eckert, G. 1966. Entwicklungsgeschichtliche und blütenanatomische Untersuchungen zum Problem der Obdiplostemonie. Bot. Jahrb. 85:523–604.
3. Labbe, A. 1966. Sur l''eperon'' de la fleur de *Pelargonium*. Bul. Soc. Bot. France (Paris) 111:321–324.
4. Miranda, R.M. and W.H. Carlson. 1980. Effect of timing and number of applications of chlormequat and ancymidol on the growth and flowering of seed geraniums. J. Amer. Soc. Hort. Sci. 105:273–277.
5. Payer, J.B. 1857. Traité d'organogénie comparée de la fleur. Librairie de Victor Masson, Paris.
6. Rickett, H.W. 1955. Materials for a dictionary of botanical terms: III. Inflorescences. Bul. Torr. Bot. Club 82:419–445.
7. Sattler, R. 1973. Organogenesis of flowers. Univ. Toronto Press, Toronto.
8. Sauer, H. 1933. Blüte and Frucht der Oxalidaceen, Linaceen, Geraniaceen, Tropaeolaceen, und Balsaminaceen. Planta 19:417–481.
9. Wyatt, R. 1982. Inflorescence architecture: how flower number, arrangement, and phenology affect pollination and fruit-set. Amer. J. Bot. 69:585–594.
10. Zanker, J. 1920. Untersuchungen über die Geraniaceen. Planta 9:681–717.

J. Amer. Soc. Hort. Sci. 108(4):600–605. 1983.

Relationship between Galactinol Synthase Activity and Sugar Composition of Leaves and Seeds of Several Crop Species

Levis W. Handley[1], David M. Pharr[1], and Roger F. McFeeters[2]

North Carolina State University, Raleigh, NC 27650

Additional index words. *Cucumis sativus*, *Glycine max*, raffinose saccharides, sucrose.

Abstract. **Galactinol synthase was assayed from leaves of 24 different accessions (20 species), maturing seeds of soybean, and cotyledons of germinating cucumber seeds. Leaf tissue contained concentrations of raffinose ranging from not detectable to 0.36 mg/g fresh weight (gfw) and stachyose ranging from not detectable to 1.39 mg/gfw. Galactinol synthase activity from leaves was correlated with the proportion of total sugar present as raffinose saccharides. In maturing soybean seeds, the appearance of galactinol synthase coincided with the biosynthesis of the galactosyl-sugars. Cucumber seeds contained high levels of raffinose and stachyose which decreased in the cotyledon during germination to a steady-state level coincident with the appearance of galactinol synthase.**

The raffinose family of oligosaccharides occurs in various plant families, many of them of horticultural importance such as *Fabaceae*, *Cucurbitaceae*, and *Brassicaceae* (7, 17, 25, 35). In legumes, these sugars often accumulate in seeds during maturation, but are not found in detectable amounts in other parts of the plant (14). Levels of 4–5% stachyose and 1–2% raffinose have been reported in soybean seeds (4, 5), where stachyose levels can often equal those of sucrose (5–7%) (2, 5). These sugars are considered major transport sugars in cucurbits (12), and they also occur in many tree species (36).

Biosynthesis of raffinose saccharides occurs by sequential transfer of galactosyl units to sucrose mediated by specific transferase enzymes (18). This is believed to occur through the intermediate galactinol, a compound composed of galactose and myo-inositol in an alpha linkage (O-α-D-galactopyranosyl-myo-inositol). Galactinol was first isolated from sugar beet by Brown and Serro (3) and later shown to be associated with the biosynthesis of raffinose saccharides by Senser and Kandler (24). Through galactinol, galactose is transferred to sucrose in the formation of raffinose and to raffinose in the formation of stachyose (19, 31) (Fig. 1).

Galactinol is synthesized by the enzyme galactinol synthase (UDP-D-galactose:inositol galactosyltransferase) which catalyzes the following reaction: UDP-galactose + myo-inositol → galactinol + UDP. It was first isolated from maturing pea seeds (8) and later isolated from *Cucurbita* leaves (34). This enzyme has also been isolated and characterized from leaves of *Cucumis sativus* (11, 22) where it has been shown to be subject to UDP

Received for publication November 1, 1982. Paper No. 8574 of the Journal Series of the North Carolina Agricultural Research Service, Raleigh. Mention of a trademark or proprietary product does not constitute a guarantee or warranty of the product by the North Carolina Agricultural Research Service or the U.S. Department of Agriculture, nor does it imply approval to the exclusion of other products that may be suitable. Supported in part by funds from USDA/SEA Cooperative Agreement No. 58-7B30-9-140. This work is a portion of a thesis to be submitted by the first author in partial fulfillment of the PhD degree. The authors wish to acknowledge the technical assistance of Harriet Sox and Susanne Armstrong in this work. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

[1]Department of Horticultural Science.

[2]Department of Food Science, U.S. Department of Agriculture, ARS, Southern Region.