Yoshihiko SATÔ* & Sumi INOUE**: Embryo sac formation of *Deutzia scabra*, *D. crenata* and *Philadelphus satsumi*

佐藤嘉彦*・井上珠実**: マルバウツギ, ウツギ及びバイカウツギの胚嚢形成

The Saxifragaceae in Engler's sense have been divided into some families by recent taxonomists. It is, therefore, thought to be composed of some heterogeneous groups. However, *Deutzia* and *Philadelphus* have been treated as closely related genera by many taxonomists. For example, Engler (1891) and Schulze-Menz (1964) treated them as two of genera of which the tribe Philadelpheae of the Saxifragaceae was composed. Hutchinson (1959) and Airy Shaw (1973) segregated the Engler's Saxifragaceae into a dozen or more families, and assigned *Deutzia* and *Philadelphus* to the family Philadelphaceae which was one of the families segregated by them, though there was a difference between their systems of classification in the delineation of the family. Cronquist (1968) segregated the Engler's Saxifragaceae into a herbaceous family (Saxifragaceae) and two woody families (Hydrangeaceae and Grossulariaceae) and he (1981) treated *Deutzia* and *Philadelphus* as two of genera of which the family Hydrangeaceae was composed.

In the Engler's Saxifragaceae, the embryological studies of such herbaceous genus as *Saxifraga* have been performed occasionally (Abe 1982), but unfortunately, on the embryology of the woody genera, we have possessed but very incomplete knowledge (Davis 1966). We have intended to perform the embryological studies of *Deutzia* and *Philadelphus*. This paper describes the results obtained from our investigations as to the formation of the embryo sac in *D. scabra* Thunb., *D. crenata* Sieb. et Zucc. and *P. satsumi* Sieb.

Materials and method At appropriate intervals extending from April to June in 1982–1984, many buds and flowers of *D. scabra* were collected from individuals growing wild in the neighbourhood of the Yokohama City University, Kanazawa-ku, Yokohama City, and those of *D. crenata* and *P. satsumi* were

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collected from individuals planted on the campus of the Yokohama National University, Hodogaya-ku, Yokohama City. All materials collected were fixed in formalin-acetic-alcohol (FAA). Then they were dehydrated in ethyl alcohol-*tert.* butyl alcohol series and embedded in paraffin or histosec (supplied by Merck & Co., Ltd.). They were sectioned serially at 6-10 μm thick and stained with Heidenhain's iron alum hematoxylin and fast green combination.

Observation Ovary and ovule. Ovaries of the three species examined were inferior. They were incompletely divided into loculi, of which the number was the same as that of carpels. *P. satsumi* had invariably four carpels, but the carpels of *D. scabra* and *D. crenata* were usually three, rarely four. Many ovules developed on the parietal placentae. In *D. scabra* and *D. crenata*, nearly all of the ovules formed were fertile. But in *P. satsumi*, the process of spore formation stopped proceeding in nearly half the number of ovules formed; those ovules became abortive. The ovule was, usually, hemianatropous (Figs. 1G, 2E) in *D. scabra* and *D. crenata* and anatropous in *P. satsumi*. The ovule of the three species examined was composed of a thin nucellus which was enclosed by one integument. Before a megasporocyte entered the meiosis or after it had just begun to divide meiotically, the integument grew up to the level of the tip of nucellus (Fig. 3A) and began to form a long canal of micropyle. In the ovule where the meiosis had just been over, the length of the canal was two to three times that of the nucellus (Figs. 1G, 2E). The integument was composed of five to seven layers of cells. The cells of the inner epidermis of integument, except cells constructing the apical portion of integument, elongated perpendicularly to the inner surface of the integument (Figs. 1I, 2G) and came to function as the integumentary tapetum. That is, the integumentary cells surrounding the canal of micropyle as well as those in contact with the nucellus or the embryo sac functioned as the tapetum. The nucellus was composed of a single axial row of cells covered by a layer of epidermal cells. The outermost cell of the axial row elongated along the axis of the nucellus and functioned as a megasporocyte without any divisions.

Embryo sac formation. The megasporocyte underwent two successive meiotic divisions. Each of them was always accompanied by wall formation. The first meiotic division (Figs. 1B, 2B) of the megasporocyte (Figs. 1A, 2A, 3A, B) was in the transverse plane and produced two dyad cells (Figs. 1C, 2C, 3C). The second division (Fig. 1D) was also transverse and took place simultaneously in

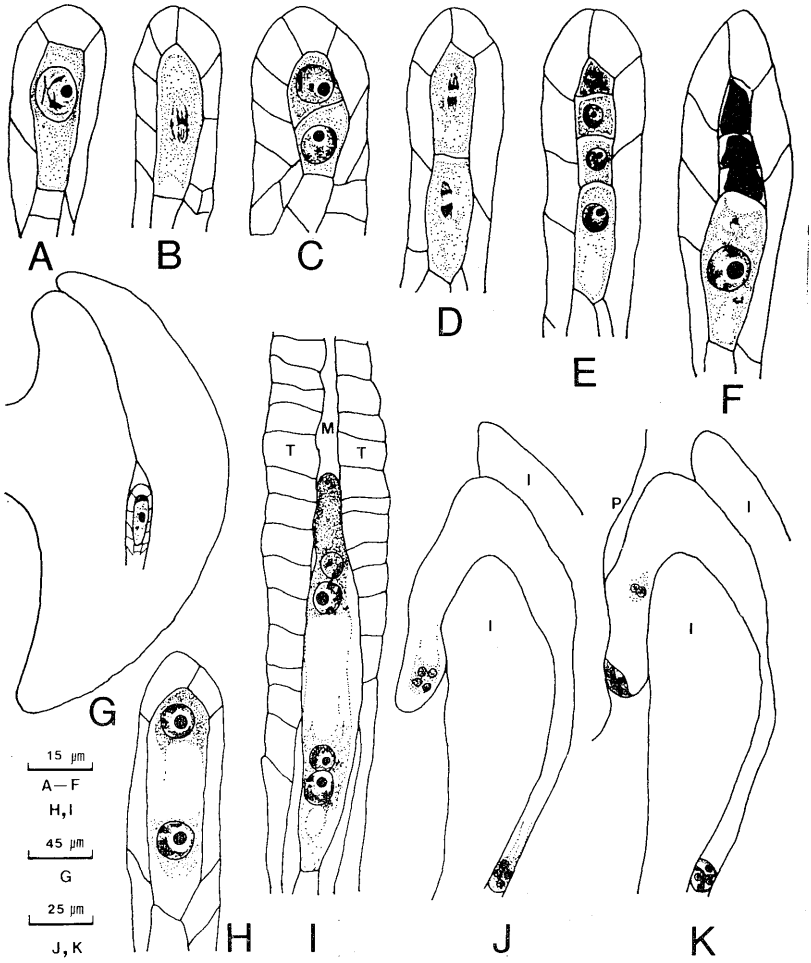

Fig. 1. Development of embryo sac in *Deutzia scabra*. A. Nucellus with megasporocyte. B. Nucellus with megasporocyte in division. C. Nucellus with dyad. D. Nucellus with two dyad cells, each in division. E. Nucellus with four-celled tetrad. F. Nucellus with functional megaspore. G. Hemianatropous ovule with functional megaspore. H. Nucellus with two-nucleate embryo sac. I. Nucellus with elongating four-nucleate embryo sac and portion of integumentary tapetum. J. Portion of ovule with eight-nucleate embryo sac, of which the micropylar portion already goes out from the micropyle. K. Portion of ovule with mature embryo sac. Details: I, integument; M, micropyle; P, placental region; T, integumentary tapetum.

two dyad cells. As the result, a linear tetrad (Figs. 1E, 2D, 3D) of megaspores was invariably produced.

A megaspore, farthest from the micropyle, of the four tetrad cells became functional, while the remaining three of them degenerated and disappeared. The functional megaspore (Figs. 1F, G, 2E, 3E) underwent the first division of its nucleus to form a two-nucleate embryo sac (Figs. 1H, 2F, 3F). The two nuclei moved apart toward the opposite poles of the embryo sac and a vacuole intervened between them. As the embryo sac elongated along the axis of the nucellus, the cytoplasm became richer around the nucleus at the micropylar end of the embryo sac than around the nucleus at the chalazal end. Usually, the two nuclei simultaneously divided to form four nuclei. In some ovules of *P. satsumi*, however, a three-nucleate embryo sac (Fig. 3G), where one nucleus lay at the micropylar end and two nuclei lay at the chalazal end, was observed. It seems that this embryo sac was produced owing to the division of the chalazal nucleus of a two-nucleate embryo sac which preceded that of the micropylar one.

The micropylar apex of the four-nucleate embryo sac (Figs. 1I, 2G, 3H) elongated rapidly and greatly to intrude into the micropylar canal. Epidermal cells of the nucellus degenerated and disappeared except a few epidermal cells at the base of nucellus. The micropylar apex of the embryo sac in the three species examined continued to elongate still more and passed through the micropylar canal. It seems that the integumentary tapetum surrounding the micropylar canal has something to do with the promotion of elongation of the embryo sac. The micropylar apex of the embryo sac went out into the ovarian locule and came into contact with the epidermal cells of the placental region. In *P. satsumi*, the embryo sac changed the course of elongation at right angles to that along which it had elongated till then, and it was only the micropylar apex that went out to the ovarian locule. On the other hand, in *D. scabra* and *D. crenata* (Fig. 2H), immediately after the micropylar apex of the embryo sac had protruded from the micropyle, the embryo sac curved sharply and continued to become longer along the epidermis of the placental region. Finally, the size of the extra-micropylar portion came to be beyond half of the embryo sac in many embryo sacs of *D. crenata*, though it was below half of the embryo sac in many ones of *D. scabra*. Before the four nuclei began to divide, in the three species the elongation of the embryo sac was nearly completed and after then the embryo sac hardly became longer.

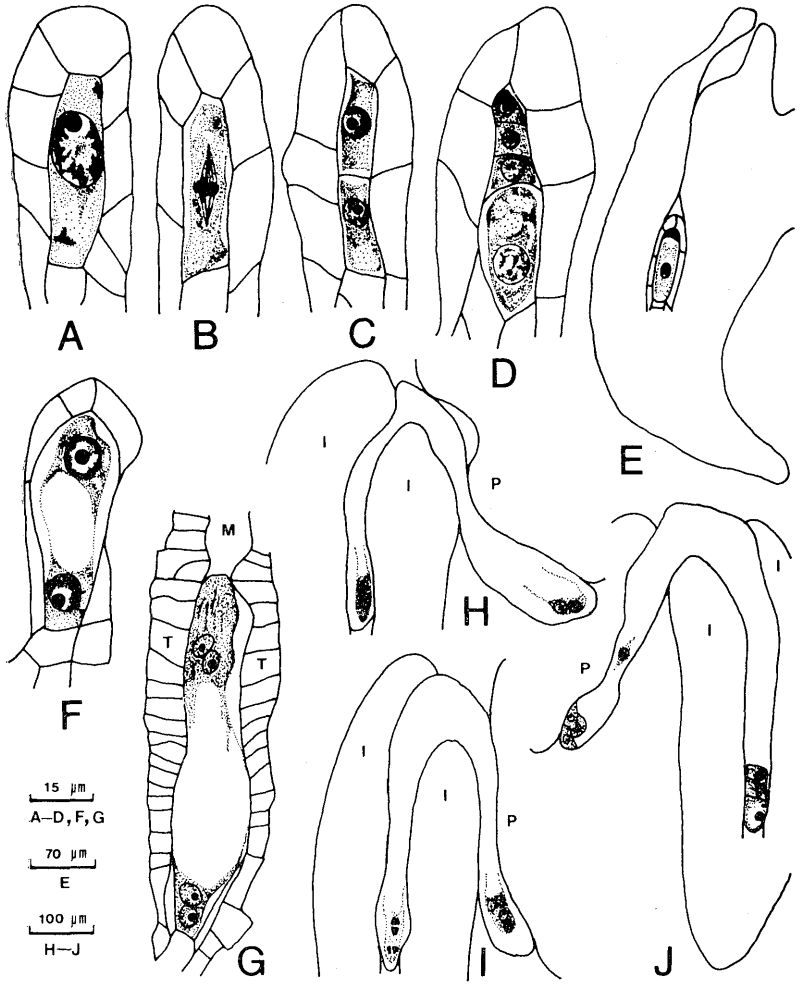

Fig. 2. Development of embryo sac in *Deutzia crenata*. A. Nucellus with megasporocyte. B. Nucellus with megasporocyte in division. C. Nucellus with dyad. D. Nucellus with four-celled tetrad. E. Hemianatropous ovule with functional megaspore. F. Nucellus with two-nucleate embryo sac. G. Nucellus with elongating four-nucleate embryo sac and portion of integmentary tapetum. H. Portion of ovules with four-nucleate embryo sac. The extra-micropylar portion exceeds half the size of the embryo sac. I. Portion of ovule with embryo sac, in which micropylar four nuclei and chalazal two nuclei in division are contained. J. Ovule with mature embryo sac. Details: I, integument; M, micropyle; P, placental region; T, integumentary tapetum.

Usually the four nuclei of the embryo sac divided simultaneously to form eight nuclei, arranged in quartets, at the micropylar and chalazal ends of the embryo sac (Fig. 1J). In some ovules of *D. crenata* (Fig. 2I), however, the chalazal two nuclei of the four-nucleate embryo sac were still in division, while the micropylar two had already divided to form four nuclei. In some ovules of *P. satsumi*, a six-nucleate embryo sac (Fig. 3I), where two nuclei lay at the micropylar end and four nuclei lay at the chalazal end, was observed. It seems that this embryo sac was produced owing to the division of the chalazal two nuclei of a four-nucleate embryo sac which preceded that of the micropylar two.

Three of the quartet at the micropylar pole of the eight-nucleate embryo sac became differentiated as an egg apparatus (Figs. 1K, 2J, 3J, K). This always lay on the outside of the ovule and consisted of an egg cell, which was flanked by two synergids. Three of the quartet at the chalazal end of the embryo sac were differentiated as antipodal cells (Figs. 1K, 2J). The two remaining nuclei migrated from the opposite ends of the embryo sac and they became polar nuclei. They usually fused near the egg apparatus in *D. scabra* (Fig. 1K) and *D. crenata* (Fig. 2J) and at the center of the embryo sac in *P. satsumi* (Fig. 3J). The antipodal cells, in many embryo sacs of *P. satsumi* (Fig. 3J), degenerated long before the polar nuclei fused, while in *D. scabra* and *D. crenata* usually they persisted after the polar nuclei had fused but they began to degenerate before fertilization.

Discussion There is little difference in the structure of ovule and in the development of embryo sac between the two species of *Deutzia* examined here. That is, the ovule is hemianatropous, unitegmic and tenuinucellate, and the megasporocyte undergoes two successive meiotic divisions to form the four-celled tetrad, of which the chalazal megaspore develops into the eight-nucleate embryo sac; the embryo sac is formed according to the monosporic eight-nucleate *Polygonum* type of development. The pattern of embryo sac formation of *Deutzia*, in principal, coincides with that of *P. satsumi* and *P. coronarius* investigated previously by Maurizon (1933). Furthermore, the embryologically salient feature common to *Deutzia* and *Philadelphus* is that the micropylar portion of the embryo sac protrudes on the outside of the ovule in greater or lesser degrees. The extra-micropylar embryo sac occurs only in very restricted genera of the angiospermous plants (Maheshwari 1950, Johri 1963). Therefore, this embryological feature common to *Deutzia* and *Philadelphus* can be considered to be one

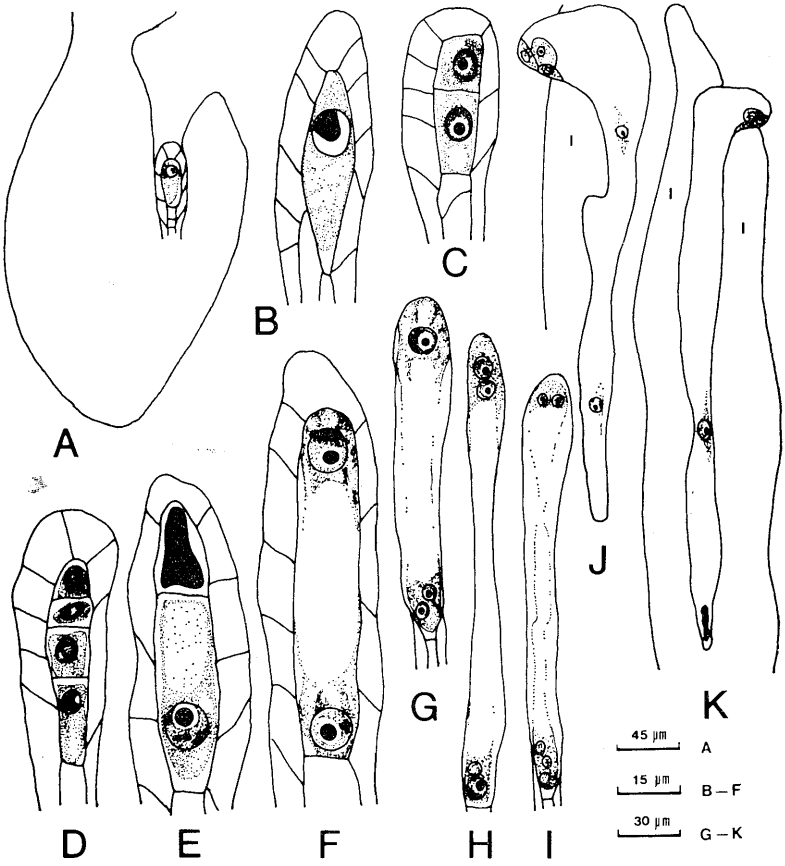

Fig. 3. Development of embryo sac in *Philadelphus satsumi*. A. Ovule which already attains to nearly anatropous condition. The megasporocyte differentiates in the nucellus. B. Nucellus with megasporocyte. C. Nucellus with dyad. D. Nucellus with four-celled tetrad. E. Nucellus with functional megaspore. F. Nucellus with two-nucleate embryo sac. G. Three-nucleate embryo sac. H. Four-nucleate embryo sac. I. Six-nucleate embryo sac. J. Mature embryo sac; two polar nuclei do not fuse yet and antipodal cells already disappear. K. Portion of ovule with mature embryo sac in which two polar nuclei already fuse and antipodal cells are already degenerating. Detail: I, integument.

of the characters which represent a near relation of the two genera. In *Torenia* and *Vandellia* of the Scrophulariaceae, there is a series of variations from the extra-micropylar to the intra-micropylar embryo sac (Yamazaki 1955). Therefore, it is conjectured that variations similar to those in the Scrophulariaceae

exist also in *Deutzia*, *Philadelphus* and their related genera such as *Hydrangea* and *Kirengeshoma*.

It is suggested from our observation that a peculiar pattern exists during the embryo sac formation in *P. satsumi*. That is, the division of the chalazal nucleus or nuclei of some developing embryo sac precedes that of the micropylar nucleus or nuclei, and further the antipodal cells degenerate and disappear long before fertilization. This is not observed during the embryo sac formation of *Deutzia*, and has not been observed during that of other previously investigated members of the Engler's Saxifragaceae (Davis 1966). Therefore, it can be considered that the short life of the antipodal cells in *P. satsumi* has something to do with the division of the chalazal nucleus or nuclei which precedes that of the micropylar nucleus or nuclei.

References

Abe, K. (1982). Embryological studies in the family Saxifragaceae (s. l.). I. Development of the ovule and embryo sac in *Saxifraga fortunei* var. *partita* (Makino) Nakai. Amer. J. Bot. **69**: 416–420. Airy Shaw, H. K. (Reviser) (1973). The families of flowering plants and ferns, by J. C. Willis. 8th ed. Cambridge University Press, London. Cronquist, A. (1968). The evolution and classification of flowering plants. Nelson, London. —— (1981). An integrated system of classification of flowering plants. Columbia University Press, New York. Davis, G. L. (1966). Systematic embryology of the angiosperms. Wiley, New York. Engler, A. (1981). Saxifragaceae. *In* Engler, A. & K. Prantl, Die natürlichen Pflanzenfamilien, III Teil. 2 Abt. a: 4–93. Hutchinson, J. (1959). The families of flowering plants, Vol. I. Dicotyledons. (2nd ed.). Clarendon Press, Oxford. Johri, B. M. (1963). Female gametophyte. *In* Maheshwari, P. (ed.), Recent advances in the embryology of angiosperms: 69–103. Catholic Press, India. Maheshwari, P. (1950). An introduction to the embryology of angiosperms. McGraw-Hill, New York. Maurizon, J. (1933). Studien über die Embryologie der Familien Crassulaceae und Saxifragaceae. Diss, Lund. (cited from Maheshwari 1950). Schulze-Menz, G. K. (1964). Reihe Rosales. *In* Melchior, H. (ed.), A Engler's Syllabus der Pflanzen familien. 12th ed. Vol. II: 193–242. Gebrüder Borntraeger, Berlin. Yamazaki, T. (1955). Notes on *Lindernia*, *Vandellia*, *Torenia* and their allied genera in Eastern Asia II. Bot. Mag. Tokyo **68**: 14–24.

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ウツギ属 (*Deutzia*) のマルバウツギ (*D. scabra*) とウツギ (*D. crenata*) 及びバイカウツギ属 (*Philadelphus*) のバイカウツギ (*P. satsumi*) の胚嚢形成過程の調査を行った。胚珠はマルバウツギとウツギでは半倒生 (hemianatropous) で，バイカウツギでは倒生 (anatropous) である。珠心は3種とも1枚の珠皮でおおわれ，薄層型 (tenuinucellate type) である。胚嚢は3種とも単胞子性8核タデ型に従って作られる。この過程で4核期の胚嚢の珠孔端は著しく伸長し，長い珠孔を抜けて胚珠の外に出る。バイカウツギでは珠孔端が胚珠の外に出るだけであるが，マルバウツギとウツギでは胚珠の外に出る部分は胚嚢のおよそ半分にも達する。胚珠の外に出る胚嚢は極く限られた属でしか知られておらず (Maheshwari 1950, Johri 1963)，ウツギ属とバイカウツギ属に共通するこの特徴は，両属の近縁性を示す特徴の一つと考えてよいであろう。

バイカウツギではしばしば2核期と4核期の胚嚢で合点側の核が珠孔側の核よりも早く分裂し，反足細胞もしばしば非常に早く退化する。マルバウツギやウツギでも，また今までに調査されたユキノシタ科（広義）の他の植物でもこのような現象は知られていない。これはバイカウツギに独特な現象と思われる。

□小室　健：**奥久慈の植物と自然の風景**　224 pp. 1984. 奥久慈植物研究友の会，茨城県大子町. ¥20,000. 奥久慈は茨城県最北の地方で福島・栃木両県に接した景色のよいことで知られた山国である。小室氏はその中心地大子町の人で，長い間植物の調査を続け，現在も同地の植物研究友の会の会長である。この本は同氏の45年にわたる成果の集成だということで，次のような内容である。八溝山・袋田と男体山・西金砂山・矢祭山・竜神峡・三鈷室山・湯沢峡・鍋足山の各地区ごとに，地域の概観，植物のリスト，その地の特記すべき植物のカラー写真入りの説明，次いで奥久慈の天然記念物，特産物，風景，植物化石など，最後に野鳥・昆虫・哺乳類などにも及んでいる。A 4判の大形のもので3段組になっており，百科事典のように紙面が充実している。写真は全部カラーで約1,800枚，5.5×4 cm と小形ながら花の大写しも生態もよく特徴が出ていて印刷も優秀である。こんなに豊富な資料を，あえて今流行の豪華版植物誌の形を取ることなしに，一巻物にまとめた見識と手際の良さは大いに称賛されるべきことだと思う。また全巻を通じて学名が1個も出ず，和名だけで処理されているのもおもしろい。この方面のフロラを調べるのにも，図鑑的に手っ取り早く植物を知るのにも便利な本である。

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