

POLLEN DIVERSITY AND EXINE EVOLUTION IN
VIBURNUM AND THE CAPRIFOLIACEAE SENSU LATO¹

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STUDIES OF POLLEN DEVELOPMENT and function (Heslop-Harrison, 1971), along with correlations between pollen morphology, incompatibility system, and mode of pollination (DeNettancourt, 1977; Lee, 1978; Plitmann & Levin, 1983), have prompted speculation about the adaptive significance of pollen characteristics (Heslop-Harrison, 1976, 1979; Lewis, 1977). At the same time considerable attention has been devoted to the related but logically separate task of determining the actual course of pollen evolution, with special emphasis on the exine (Erdtman, 1966; Walker & Doyle, 1975; Ferguson & Muller, 1976; Nowicke & Skvarla, 1979). A particular hypothesis about pollen evolution is usually established by considering pollen diversity in the context of presumed relationships. Pollen characters are mapped onto a classification (which is usually based on many other kinds of characters), and the most plausible sequence of evolutionary events for the pollen is established in this context. This procedure is basically sound, but clearly the results obtained can be no better than the hypothesis of relationships employed. Unfortunately, relationships have not yet been rigorously established for most plant groups, and present classifications do not always reflect these accurately or unambiguously. Thus, although considerable progress has been made in tracing the course of pollen evolution, the level of resolution has not always been very satisfactory.

Cladistic analysis can be a powerful tool for the study of character evolution. A cladogram provides a test of the congruence of characters and establishes the simplest hypothesis of the direction and sequence of character transformations. In addition, it is a rigorous means of assessing the nature and extent of homoplasy—i.e., of convergent evolution and reversal. One can also determine the relative timing of the origin of traits, information that is critical for the historical analysis of adaptation. Thus it is possible to establish the level at which a particular character transformation (e.g., from small to large pollen) occurred relative to changes in other characters of interest (e.g., style length).

Unfortunately, cladograms are now available for only a small number of plant groups, and with only a few exceptions (e.g., Kress & Stone, 1983) pollen evolution has not been studied in a cladistic context. The primary purpose of this paper is to provide a cladistic analysis of exine evolution in *Viburnum* L. This genus is especially well suited for the purpose for three reasons. First, its pollen is quite well known from previous studies, and the present survey sig-

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nificantly increases the number of species sampled and gives a clear understanding of the taxonomic distribution of pollen characters. We can now be quite confident that we know the range and pattern of pollen variation in the genus. Second, a corroborated hypothesis of the cladistic relationships of *Viburnum* to other genera is available (Donoghue, 1983b), enabling evaluation of the polarity of pollen characters using outgroup analysis (Maddison *et al.*, 1984). Finally, a preliminary cladistic analysis of the genus has been carried out (Donoghue, 1983a), making it possible to assess the congruence of pollen characters with other characters and to establish the most parsimonious hypothesis of exine evolution. An equally rigorous analysis of pollen evolution in other Caprifoliaceae is not yet possible. However, cladistic reasoning can still be applied, and it is possible to generate preliminary hypotheses that can be tested in the future.

Throughout this paper I refer to Caprifoliaceae *sensu stricto* (*s.s.*) and Caprifoliaceae *sensu lato* (*s.l.*). The family Caprifoliaceae *s.s.* is equivalent to the subfamily Caprifolioideae of Hara (1983) and contains 11 genera that he assigned to four tribes: *Leycesteria* Wallich and *Lonicera* L. of the Caprifolieae; *Diervilla* Miller and *Weigela* Thunb. of the Diervilleae; *Triosteum* L. of the Triosteae; and *Abelia* R. Br., *Dipelta* Maxim., *Heptacodium* Rehder, *Kolkwitzia* Graebner, *Linnaea* L., and *Symphoricarpos* Duhamel of the Linnaeae. The Caprifoliaceae *s.l.* consist of the Caprifoliaceae *s.s.* plus *Viburnum*, *Sambucus* L., and *Adoxa* L. The last genus is frequently placed in its own family, Adoxaceae, but many characters point to a close relationship between *Adoxa* and *Sambucus*, and of these genera to *Viburnum* (Donoghue, 1983b). It is therefore essential to include *Adoxa* in evolutionary studies involving *Sambucus* and *Viburnum*.

Two new species, *Adoxa omeiensis* Hara (Wu, 1981; Hara, 1981, 1983) and *Sinadoxa corydalifolia* C. Y. Wu, Z. L. Wu, & R. F. Huang (Wu *et al.*, 1981) have recently been described in the Adoxaceae. These resemble *Adoxa moschatellina* L. and should probably also be included in the Caprifoliaceae *s.l.* They are excluded here simply because they are very poorly known and their pollen was unavailable for study. Since Wu's (1981) scanning electron micrographs show that the pollen of both new species is very similar to that of *Adoxa* and *Sambucus*, the results of the present analysis would not have been significantly altered by the inclusion of these taxa.

POLLEN DIVERSITY IN THE CAPRIFOLIACEAE S.L.

PREVIOUS STUDIES

Light microscopic (LM) studies have revealed considerable variation in pollen morphology in the Caprifoliaceae *s.l.*, and to a lesser extent within *Viburnum* (see Erdtman, 1966, and Thanikaimoni, 1972, for references to the early literature; see also Punt *et al.*, 1974; Reitsma & Reuvers, 1975). Punt and colleagues (1974) published scanning electron micrographs (SEMGs) of the pollen of three species, Rader (1976) used the SEM to study several species in *Viburnum* sect. LENTAGO, Reitsma and Reuvers (1975) published SEMGs of *Adoxa moschatellina*, and Adams and Morton (1979) presented SEMGs of

18 species in five genera. More recently, Böhnke-Gütlein and Weberling (1981) published the first part (tribes Sambuceae, Viburneae, and Diervilleae) of a careful and extensive LM and SEM survey of the pollen of the Caprifoliaceae, and Hara (1983) included SEMGs of the pollen of 30 specimens in his treatment of the Caprifoliaceae of Japan.

Unfortunately and despite considerable previous study and the evident diversity of pollen in the Caprifoliaceae *s.l.*, pollen characters have been used little—or uncritically—by phylogenists. Because most palynological work on the group has been conducted within the last decade, information pertaining to pollen morphology is entirely lacking from the most recent comprehensive revision of the tribes of the family (Fukuoka, 1972). It has been noted, however, that the pollen of *Adoxa* is very similar to that of *Sambucus* (Cronquist, 1968, 1981) and that the pollen grains of *Viburnum* and *Sambucus* are similar, but that all differ markedly from the pollen of the four tribes of Caprifoliaceae *s.s.* (Ferguson, 1966; Lewis, pers. comm. in Hillebrand & Fairbrothers, 1970; also cited in Bohm & Glennie, 1971). The genera of the Caprifoliaceae *s.s.* are palynologically similar (Erdtman, 1966; Lewis & Fantz, 1973), but there is significant variation in pollen size (apparently correlated with chromosome number) in *Symphoricarpos* (Bassett & Crompton, 1970), and pollen differences in *Abelia* (Ikuse & Kurosawa, 1954; Erdtman, 1966, 1969) prompted the segregation of the genus *Zabelia* Makino. Böhnke-Gütlein and Weberling (1981) discussed some taxonomic implications of pollen diversity in the family but reached few conclusions about phylogenetic relationships or the evolution of pollen morphology in the group. However, additional discussion is expected in the second portion of their survey (MS in press, *vide* Böhnke-Gütlein & Weberling, 1981).

MATERIALS AND METHODS

Pollen from mature anthers was affixed to aluminum stubs with double-stick tape. All samples are vouchered by annotated herbarium specimens (see TABLES 1, 2), most of which are deposited in the Harvard University Herbaria (A or GH). Prepared stubs were coated with approximately 200 Å of gold-palladium in two 1.5-minute steps using a Technics Hummer II sputter coater. Specimens were examined with an AMR model 1000a scanning electron microscope, in the secondary electron mode, using accelerating voltages up to 20 kv. SEMGs were recorded on Polaroid Type 55 P/N 4 × 5" film. All photomicrographs were taken at the Museum of Comparative Zoology Scanning Electron Microscope Laboratory, Harvard University.

The method of preparation of pollen grains for the SEM can sometimes significantly affect the results obtained (Hanks & Fairbrothers, 1970). In the initial phases of this study, pollen was acetolyzed (according to Erdtman, 1960) prior to scanning. However, when it was found that unacetolyzed and acetolyzed pollen of *Viburnum* differed little (i.e., "Pollenkitt" is limited), acetolysis was discontinued. The transmission electron microscope (TEM) was not utilized in this study, but cross sections of the exine were obtained for SEM study by spreading pollen on a glass plate, cutting it with a razor blade, and transferring it with a brush to a stub.

TABLE 1. The pollen of *Viburnum*.

TAXON ¹	POLLEN DIMENSIONS ²			POLLEN SHAPE ⁴	POLLEN TYPE ⁵	VOUCHER SPECIMEN ⁶	
	Polar axis (P) in μm	Equatorial axis (E) in μm	P/E ³			Locality	Collection
<i>Odontotinus</i> Rehder							
<i>V. acerifolium</i> L.	---	---	---	---	(I)a	U.S.A.: Connecticut	Churchill s.n., 1952 (MSC)
<i>V. dentatum</i> L.	---	---	---	---	(I)a	U.S.A.: New Jersey	Hermann 4240 (MICH)
<i>V. dilatatum</i> Thunb.	16.5(17.3)18.6 s = 0.576	16.5(17.7)18.6 s = 0.785	0.98	0-S	Ia	Japan: Izu Peninsula	Ohashi, Nakaike, & Tateishi 70627 (A)
<i>V. ellipticum</i> Hooker	22.6(24.4)25.8 s = 0.840	19.5(22.6)24.7 s = 1.427	1.08	P-S	Ia	U.S.A.: Oregon	Hunt 36 (A)
<i>V. foetidum</i> Wallich	18.6(20.7)21.6 s = 1.112	12.4(14.0)15.5 s = 0.750	1.48	EU	Ia	China: Yunnan	Forrest 18129 (A)
<i>V. japonicum</i> (Thunb.) Sprengel	23.4(24.5)26.5 s = 0.879	17.3(18.6)20.4 s = 0.821	1.31	SP	Ia	Japan: Kyushu	Ichikawa 26 (A)

<u>V. kansuense</u> Batalin	—	—	—	(I)a	China: Sichuan	Rock 16440 (US)
<u>V. orientale</u> Pallas	17.5(18.6)19.6 s = 0.837	16.5(18.1)19.6 s = 0.789	1.03	Ia	Turkey	Balls 1927 (A)
<u>V. rafines-</u> <u>quianum</u> Schultes	—	—	—	(I)a	U.S.A.: Michigan (?)	Penfield s.n., 9 June 1909 (MICH)
<u>V. sempervirens</u> K. Koch	24.7(26.7)28.8 s = 0.930	16.5(17.7)18.6 s = 0.718	1.51	Ia	China: Guandong	Gressitt 1247 (A)
<u>V. wrightii</u> Miq.	22.7(25.2)26.8 s = 1.102	15.5(16.5)18.6 s = 0.775	1.53	Ia	Japan: Hizen	Hatusima 4206 (A)
<u>Oreinotinus</u> (Oersted) Bentham & Hooker						
<u>V. acutifolium</u> Bentham	—	—	—	(I)a	Mexico: Oaxaca	Stevens, Donoghue, & Scott 2492 (MSC)
<u>V. caudatum</u> Greenman	—	—	—	(I)a	Mexico, sine loco	Gutierrez 54 (MICH)
<u>V. ciliatum</u> Greenman	—	—	—	(I)a	Mexico: Hidalgo	Maury 5786 (NY)

TABLE 1 (continued).

TAXON ¹	POLLEN DIMENSIONS ²			POLLEN SHAPE ⁴	POLLEN TYPE ⁵	VOUCHER SPECIMEN ⁶	
	Polar axis (P) in μ m	Equatorial axis (E) in μ m	P/E ³			Locality	Collection
<u>V. costaricanum</u> (Oersted) Hemsley	—	—	—	—	(I)a	Costa Rica: San José	Lellinger & White 1588 (F)
<u>V. hartwegii</u> Bentham	—	—	—	—	(I)a	Mexico: Chiapas	Stevens, Donoghue, & Scott 2423 (MSC)
<u>V. jucundum</u> Morton	—	—	—	—	(I)a	Mexico: Chiapas	Stevens, Donoghue, & Scott 2350 (MSC)
<u>V. loeseneri</u> Graebner	—	—	—	—	(I)a	Mexico: Michoacán	Stevens, Donoghue, & Scott 2547 (MSC)
<u>V. mendax</u> Morton	—	—	—	—	(I)a	Guatemala: Huehuetenango	Skutch 1065 (US)
<u>V. microcarpum</u> Schlecht. & Cham.	23.7(25.4)27.8 s = 1.337	18.5(20.1)22.7 s = 1.471	1.26	SP	Ia	Mexico: Veracruz	Ventura A. 819 (ENCB)

<u>V. stenocalyx</u> (Oersted) Hemsley	—	—	—	(I)a	Mexico: Puebla	<u>Purpus 163</u> (US)
<u>V. sulcatum</u> (Oersted) Hemsley	—	—	—	(I)a	Mexico: Oaxaca	<u>Rzedowski</u> <u>12436 (ENCB)</u>
<u>V. tinoides</u> L.	—	—	—	(I)a	Colombia: Cundina- marca	<u>Barclay,</u> <u>Juaibioy, &</u> <u>Gama 3146</u> (US)
<u>V. triphyllum</u> Bentham	—	—	—	(I)a	Ecuador: Azuay	<u>Camp E-3900</u> (MICH)
<u>V. venustum</u> Morton	—	—	—	(I)a	Costa Rica: Alajuela	<u>Jiménez 3947</u> (F)
<u>Solenotinus</u> DC.						
<u>V. brachybotryum</u> Hemsley	20.6(22.3)23.7 s = 0.871	19.6(20.3)21.6 s = 0.617	1.10	P-S	China: Yunnan	<u>Henry 12790A</u> (A)
<u>V. erubescens</u> Wallich ex DC.	20.6(22.4)23.7 s = 0.744	18.6(20.3)21.6 s = 0.798	1.10	P-S	Western China	<u>Wilson 3734</u> (A)
<u>V. farreri</u> Stearn	22.6(23.9)24.7 s = 0.861	16.5(17.7)18.6 s = 0.679	1.35	EU	China: Gansu	<u>Rock 12142</u> (A)
<u>V. henryi</u> Hemsley	26.8(28.5)30.9 s = 1.249	21.6(22.8)24.7 s = 1.115	1.25	SP	China: Hubei	<u>Wilson 1071</u> (A)

TABLE 1 (continued).

TAXON ¹	POLLEN DIMENSIONS ²			P/E ³	POLLEN SHAPE ⁴	POLLEN TYPE ⁵	VOUCHER SPECIMEN ⁶	
	Polar axis (P) in μ m	Equatorial axis (E) in μ m	s				Locality	Collection
<u>V. odoratissimum</u> Ker Gawler	22.7(23.9)24.7 s = 0.883	20.6(22.4)23.7 s = 0.840		1.07	P-S	Ia	Philippines: Mountain Province	Alcacid 70 (A)
<u>V. odoratissimum</u> Ker Gawler	---	---	---	---	---	(I)a	China: Sichuan	H. H. Hu 770 (A)
<u>V. oliganthum</u> Batalin	26.8(28.8)30.9 s = 1.172	23.7(25.0)26.8 s = 1.077		1.15	SP	Ia	China: Sichuan	H. Smith 1961 (A)
<u>V. sieboldii</u> Miq.	---	---	---	---	---	(I)a	Japan: Musashi	Maruyama 10 (MICH)
<u>V. suspensum</u> Lindley	22.7(23.8)25.8 s = 1.112	20.6(22.0)22.7 s = 0.770		1.08	P-S	Ia	Japan: Kyushu	Hatusima 864 (GH)
<u>Tinus</u> (Miller) C. B. Clarke								
<u>V. atrocyaneum</u> C. B. Clarke	23.7(25.2)26.8 s = 0.960	19.6(21.0)23.7 s = 1.386		1.20	SP	Ia	China: Xizang	Rock 8905 (A)
<u>V. cinnamomi-folium</u> Rehder	21.6(24.6)26.8 s = 1.325	16.5(17.6)18.6 s = 0.929		1.40	EU	Ia	China: Sichuan	Yü 539 (A)

<u>V. davidii</u> Franchet	25.8(27.4)28.8 s = 0.828	22.7(24.7)25.8 s = 0.918	1.11	P-S	Ia	Western China	<u>Wilson 3728</u> (A)
<u>V. propinquum</u> Hemsley	17.5(19.0)20.6 s = 1.090	16.5(17.3)18.6 s = 0.901	1.10	P-S	Ia	China: Hubei	<u>Henry 3415</u> (A)
<u>V. tinus</u> L.	36.1(38.8)42.3 s = 1.700	22.7(23.5)24.7 s = 0.861	1.65	EU	Ia	Italy: Istria	<u>Marchesetti</u> <u>2752 (GH)</u>
<u>Tomentosa Nakai</u>							
<u>V. hanceanum</u> Maxim.	22.7(24.7)26.8 s = 1.036	14.4(15.8)16.5 s = 0.729	1.56	EU	Ia	Hong Kong	<u>Chun 5314 (A)</u>
<u>V. plicatum</u> Thunb.	---	---	---	---	(I)a	Japan: Sagami	<u>Ohwi &</u> <u>Okamoto 502</u> (MICH)
<u>Opulus DC.</u>							
<u>V. edule</u> (Michaux) Raf.	18.6(20.9)22.7 s = 1.253	15.5(16.5)17.5 s = 0.755	1.27	SP	Ia	U.S.A.: Washing- ton	<u>Suksdorf 2063</u> (A)
<u>V. sargentii</u> Koehne	21.6(22.9)24.7 s = 0.797	19.6(20.7)21.6 s = 0.915	1.11	P-S	Ia	Japan: Shinano	<u>Furuse s.n.,</u> <u>20 June 1961</u> (A)
<u>V. sargentii</u> Koehne	---	---	---	---	(I)?	Japan: Iwashiro	<u>Furuse s.n.,</u> <u>9 June 1958</u> (A)

TABLE 1 (continued).

TAXON ¹	POLLEN DIMENSIONS ²			P/E ³	POLLEN SHAPE ⁴	POLLEN TYPE ⁵	VOUCHER SPECIMEN ⁶	
	Polar axis (P) in μ m	Equatorial axis (E) in μ m	s				Locality	Collection
<u>Pseudotinus</u> C. B. Clarke								
<u>V. cordifolium</u> Wallich ex DC.	26.8(28.9)30.9 s = 1.427	18.6(20.9)22.7 s = 1.045		1.38	EU	Ic	China: Yunnan	Forrest 11892 (A)
<u>V. furcatum</u> Blume	17.5(19.5)21.6 s = 1.256	17.5(18.2)18.6 s = 0.557		1.07	P-S	Ia	Japan: Niigata	Togashi 7145 (A)
<u>V. lantanoides</u> Michaux	17.5(18.4)19.6 s = 0.718	17.5(19.3)20.6 s = 0.831		0.95	O-S	Ia	U.S.A.: Massa- chusetts	Andrews s.n., 1897 (GH)
<u>Megalotinus</u> (Maxim.) Rehder								
<u>V. cylindricum</u> Ham. ex D. Don	24.7(26.3)30.9 s = 2.199	19.5(20.7)21.6 s = 0.516		1.27	SP	Ia	China: Yunnan	Forrest 11513 (A)
<u>V. cylindricum</u> Ham. ex D. Don	—	—		—	—	(I)a	Thailand: Chiang Mai	Iwatsuki, Koyama, Fukuoka, & Nalampoorn 9424 (A)

<u>V. punctatum</u> Ham. ex D. Don	20.6(21.2)23.7 s = 1.088	19.5(21.3)22.7 s = 0.854	0.99	0-S	Ib	China: Sichuan	Schneider 691 (A)
<u>V. ternatum</u> Rehder	24.7(26.4)29.9 s = 1.645	21.6(22.9)26.8 s = 1.381	1.15	SP	Ia	China: Guizhou	Teng 90584 (A)
<u>Viburnum</u>							
<u>V. burejaeticum</u> Regel & Herder	20.6(22.1)22.7 s = 0.687	23.7(25.3)26.8 s = 0.960	0.87	SO	Ic	N. Korea: N. Hamkyong	Ishidoya s.n., 1918 (A)
<u>V. carlesii</u> Hemsley	17.5(19.8)21.6 s = 1.220	18.6(20.3)21.6 s = 0.978	0.98	0-S	Ib	Japan: Honshu	Togashi 7761 (A)
<u>V. lantana</u> L.	—	—	—	—	(I)c	England, sine loco	Fisher s.n., 1883 (MICH)
<u>V. macrocephalum</u> Fortune	23.7(24.5)25.8 s = 0.808	24.7(25.9)27.8 s = 0.892	0.95	0-S	Ib	China: Zhejiang	Chiao 7962 (A)
<u>V. macrocephalum</u> Fortune	—	—	—	—	(I)b	China: Hubei	Wilson 1835 (A)
<u>V. mongolicum</u> (Pallas) Rehder	29.9(32.2)35.1 s = 1.437	20.6(23.2)24.7 s = 1.008	1.39	EU	Ic	China: Gansu	Rock 12480 (A)
<u>V. rhytidophyllum</u> Hemsley	—	—	—	—	(I)c	China: Hubei	Wilson 654 (US)
<u>V. shensianum</u> Maxim.	24.7(25.3)26.8 s = 0.835	21.6(23.7)24.7 s = 1.033	1.07	P-S	Ib	China: Shanxi	Tang 776 (A)

TABLE 1 (continued).

TAXON ¹	POLLEN DIMENSIONS ²			P/E ³	POLLEN SHAPE ⁴	POLLEN TYPE ⁵	VOUCHER SPECIMEN ⁶	
	Polar axis (P) in μ m	Equatorial axis (E) in μ m	s				Locality	Collection
<u>V. urceolatum</u> Sieb. & Zucc.	20.6(21.8)23.7 s = 1.060	19.6(20.6)21.6 s = 0.539		1.06	P-S	Ia	Japan: Kyushu	Tashiro s.n., 1917 (A)
<u>V. utile</u> Hemsley	20.6(22.7)23.7 s = 0.879	22.7(24.5)25.8 s = 0.989		0.93	0-S	Ib	China: Hubei	H. C. Chow 145 (A)
<u>V. veitchii</u> C. H. Wright	17.5(18.6)19.6 s = 0.561	19.6(20.5)21.6 s = 0.639		0.91	0-S	Ic	China: Zhejiang	Lingnan Univ. Herb. 78294 (A)
<u>Lentago</u> DC.								
<u>V. elatum</u> Bentham	25.8(27.1)28.8 s = 1.032	19.6(21.3)22.7 s = 1.015		1.27	SP	Ic	Mexico: Chiapas	Alexander 1049 (NY)
<u>V. nudum</u> L.	—	—		—	—	(I)b	U.S.A.: Florida	Churchill s.n., 1956 (MSC)
<u>V. nudum</u> var. <u>cassinoides</u> (L.) Torrey & Gray	28.8(33.8)36.1 s = 1.906	19.6(22.3)24.7 s = 1.438		1.52	EU	Ic	U.S.A.: New Hamp- shire	Russell s.n., 1924 (GH)

<u>V. prunifolium</u> L.	34.0(35.5)38.1 s = 1.214	19.6(21.0)22.7 s = 1.222	1.69	EU	Ic	U.S.A.: West Virginia	<u>Bartholomew</u> <u>1518 (GH)</u>
<u>V. prunifolium</u> L.	—	—	—	—	(I)c	U.S.A.: Missouri	<u>Bush 7939</u> <u>(GH)</u>
<u>V. rufidulum</u> Raf.	—	—	—	—	(I)c	U.S.A.: Florida	<u>Godfrey 61912</u> <u>(MSC)</u>

¹Species arranged alphabetically within sections sensu Hara (1983); sections arranged according to pollen type as in Plates I-XI.

²Measurements made from scanning electron micrographs as described under materials and methods above. First figure = smallest grain; second figure = mean; third figure = largest grain; s = standard deviation; sample size = 15 grains; dash = measurement not obtained.

³Mean polar length (P) divided by mean equatorial length (E).

⁴Shapes classified according to Walker and Doyle (1975): EU = euprolate; O-S = oblate-spheroidal; P-S = prolate-spheroidal; SO = suboblate; SP = subprolate.

⁵Size-shape class (I) and exine structure-sculpture class (a, b, c) define pollen type (see text). Size-shape class in parentheses if grain size determined solely by comparison with grains of known size.

⁶Locality data consist of country and state or province provided on herbarium label. Chinese provinces spelled according to the Pinyin system. Herbaria: Arnold Arboretum (A), Escuela Nacional de Ciencias Biológicas (ENCB), Field Museum of Natural History (F), Gray Herbarium (GH), University of Michigan Herbarium (MICH), Beal-Darlington Herbarium, Michigan State University (MSC), New York Botanic Garden (NY), and U. S. National Herbarium (US).

⁷This grain from unopened (not fully mature?) anther not assigned to an exine structure-sculpture class.

TABLE 2. The pollen of the Caprifoliaceae s.l. (except Viburnum).¹

TAXON ²	POLLEN DIMENSIONS ³			P/E ⁴	POLLEN SHAPE ⁵	POLLEN TYPE ⁶	VOUCHER SPECIMEN ⁷	
	Polar axis (P) in μ m	Equatorial axis (E) in μ m	s				Locality	Collection
Adoxaceae Trautv.								
<u>Adoxa moschataellina</u> L.	32.0(33.9)37.1 s = 1.577	15.5(18.2)19.6 s = 1.096		1.86	EU	Ia	Japan: Shinano	Furuse s.n., 15 May 1961 (A)
Caprifoliaceae								
A. L. Juss.								
Sambucoideae								
(Endl.) Luerssen								
<u>Sambucus pubens</u> Michaux	22.7(24.2)25.8 s = 0.847	12.4(13.5)14.4 s = 0.516		1.79	EU	Ia	U.S.A.: Massachusetts	Forbes 3433 (GH)
Caprifolioideae								
Caprifoliaceae								
<u>Leycesteria formosa</u> Wallich	43.6(46.4)48.7 s = 1.783	48.7(51.6)56.4 s = 2.535		0.90	0-S	IId	China: Sichuan	Schneider 1394 (A)
<u>L. gracilis</u> (Kurz) Airy Shaw	—	—		—	—	(II)d	China: Yunnan	Forrest 9377 (A)

<u>Lonicera</u> <u>chrysantha</u> Turcz.	---	---	---	(II)d	China: Weichang	<u>Purdum 6b</u> (A)
<u>L. semper-</u> <u>virens</u> L.	---	---	---	(II)d	U.S.A.: Virginia	<u>Fernald &</u> <u>Long 7973</u> (GH)
<u>L. tatarica</u> L.	---	---	---	(II)d	Canada: Québec	<u>Bro. Victorin</u> <u>181</u> (A)
Diervillieae C. Meyer						
<u>Diervilla</u> <u>lonicera</u> Miller	30.9(34.4)37.1 s = 2.202	36.1(39.0)41.2 s = 1.652	0.88	II(f) ⁸	Canada: Newfound- land	<u>Jamison(?)</u> s.n., 1930 (GH)
<u>Weigela</u> <u>florida</u> (Bunge) DC.	41.0(42.2)43.6 s = 1.370	43.6(46.8)51.3 s = 2.122	0.90	II f	S. Korea: Anyang	<u>Moran 4257</u> (GH)
Triosteae Hutch.						
<u>Triosteum</u> <u>aurantiacum</u> Bickn.	51.3(53.8)56.4 s = 2.208	56.4(60.2)64.1 s = 2.335	0.89	IIe	U.S.A.: Pennsyl- vania	<u>Pennell s.n.</u> , <u>1924</u> (GH)
<u>T. perfoliatum</u> L.	---	---	---	(II)e	U.S.A.: Kansas	<u>McGregor</u> <u>14287</u> (GH)

TABLE 2 (continued).

TAXON ²	POLLEN DIMENSIONS ³				POLLEN SHAPE ⁵	POLLEN TYPE ⁶	VOUCHER SPECIMEN ⁷	
	Polar axis (P) in μm	Equatorial axis (E) in μm	P/E ⁴				Locality	Collection
Linnaeaceae Dumort.								
<u>Abelia</u> <u>spathulata</u> Sieb. & Zucc.	45.0(47.0)50.0 s = 2.297	50.0(55.8)60.0 s = 3.493	0.84	SO	IId	Japan: Kai	Furuse s.n., 7 May 1957 (A)	
<u>Dipelta</u> <u>yunnanensis</u> Franchet	43.6(49.1)53.8 s = 2.728	43.6(49.2)56.4 s = 2.582	0.99	O-S	IId	China: Sichuan	Rock 16150 (A)	
<u>Heptacodium</u> <u>jasmnoides</u> Airy Shaw	47.5(50.0)52.5 s = 1.636	50.0(51.5)55.0 s = 2.275	0.97	O-S	IId	China: Zhejiang	Keng 1068 (A)	
<u>Kolkwitzia</u> <u>amabilis</u> Graebner	---	---	---	---	(II)d	U.S.A.: Massa- chusetts (native to China)	Rehder, Arnold Arb. 6475 (GH)	
<u>Linnaea</u> <u>borealis</u> L.	33.0(35.4)37.1 s = 1.423	35.1(36.8)38.1 s = 1.182	0.96	O-S	IId	Canada: Labrador	Woodworth 388 (GH)	
<u>Symphoricarpos</u> <u>albus</u> (L.) Blake	26.8(27.5)28.8 s = 1.154	30.9(32.5)34.0 s = 1.180	0.85	SO	IIE	Canada: Ontario	Pease & Bean 26146 (GH)	

Valerianaceae
Batsch

Nardostachys 46.2(49.9)56.4 51.3(54.0)56.4 0.92 0-S IID China: Rock 14168
jatamansii s = 3.158 s = 1.939 Xizang
(D. Don) DC.

¹Caprifoliaceae s.l. includes Adoxaceae (Donoghue, 1983b); one species of Valerianaceae included for comparison.

²Species arranged alphabetically within families, subfamilies, and tribes sensu Hara (1983).

³Measurements made from scanning electron micrographs as described under materials and methods above. First figure = smallest grain; second figure = mean; third figure = largest grain; s = standard deviation; sample size = 15 grains; dash = measurement not obtained.

⁴Mean polar length (P) divided by mean equatorial length (E).

⁵Shapes classified according to Walker and Doyle (1975): EU = euprolate; O-S = oblate-spheroidal; SO = suboblate.

⁶Size-shape class (I, II) and exine structure-sculpture class (a, d, e, f) define pollen type (see text). Size-shape class in parentheses if grain size determined solely by comparison with grains of known size.

⁷Locality data consist of country and state or province provided on herbarium label. Chinese provinces spelled according to the Pinyin system. Herbaria: Arnold Arboretum (A) and Gray Herbarium (GH).

⁸Cross section of exine not seen.

Pollen of 63 *Viburnum* species and 18 species of 14 other genera was examined. In preliminary investigations a number of specimens were studied from different parts of the geographic range of several species (e.g., *Viburnum acutifolium*, *V. hartwegii*, *V. prunifolium*, *V. elatum*, *Sambucus pubens*, and *Diervilla lonicera*). There was little variation in the size, shape, structure, and sculpturing of the grains within or between individuals of a species (with the exception of one specimen of *V. sargentii*—see footnote 7, TABLE 1, and PLATE VB). Therefore, for the majority of species, pollen from only one specimen was photographed and measured.

All size measurements were obtained from SEMGs of air-dried, unacetolyzed pollen. Low-magnification ($\times 200$ or $\times 500$) SEMGs were taken to include at least 15 grains. By means of the bar scale, micrometers were converted to millimeters, and polar and equatorial measurements were obtained directly from the photographs. The bar scale is presumed to be accurate to within 5–10 percent. Sample sizes were small; however, standard deviations were uniformly low. Grain sizes of different individuals of the same species were not compared, so statistical significance was not calculated. The measurements presented in TABLES 1 and 2 can therefore serve only as rough indicators of grain size. Measurements made by this method were compared in several instances to those of acetolyzed grains mounted in glycerin jelly, as well as to published LM measurements. In all cases there was good correspondence between SEM and LM measurements.

The terminology used throughout this paper is taken from Walker and Doyle's (1975) modification and consolidation of the terminologies developed by Erdtman (1969) and Faegri and Iversen (1975). Precise definitions of some terms, especially those relating to exine sculpturing, are given by Reitsma (1970).

POLLEN MORPHOLOGY

SIZE-SHAPE CLASSES. The range of pollen sizes, the mean size, and the standard deviation are recorded in TABLES 1 and 2 for 52 of the 81 species examined. Quotients of polar/equatorial (P/E) axis-length were obtained from the mean sizes, and these were converted into shape classes using Walker and Doyle's (1975) classification.

In FIGURE 1 mean polar length is plotted against mean equatorial length for each species measured. There is a wide range of pollen sizes, but within this range there are correlated differences in grain length and width, with the wider grains tending to be longer. In addition, shape and size differences are clearly correlated. Perfectly spherical grains would lie along the 45° line in FIGURE 1, with oblate grains above this line and prolate ones below it. Note that the larger grains are oblate, while the smaller ones are generally prolate. There are several exceptions to this correlation in *Viburnum*, especially within sect. *VIBURNUM*, and the possible significance of these is discussed below.

On the basis of the correlation between size and shape, two size-shape classes are recognized. Pollen in class I ranges from 16.5 (*Viburnum dilatatum*) to 42.3 μm long (*V. tinus*), and from 12.4 (*V. foetidum* and *Sambucus pubens*) to 26.8 μm wide (*V. oliganthum*, *V. ternatum*, and *V. burejaeticum*). The mean length

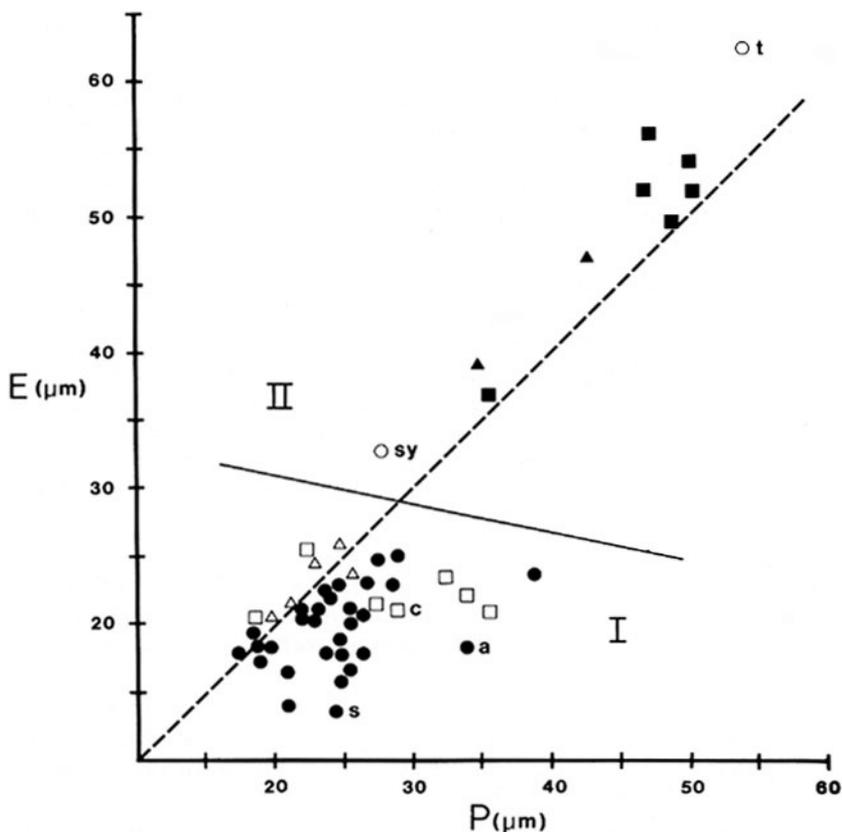


FIGURE 1. Pollen size-shape and structure-sculpture classes in Caprifoliaceae *s.l.* P = length of polar axis, E = length of equatorial axis, 45° dashed line = spherical grains, I and II = size-shape classes. Symbols for structure-sculpture classes: closed circles = class a, open triangles = class b, open squares = class c, closed squares = class d, open circles = class e, closed triangles = class f. a = *Adoxa moschatellina*, s = *Sambucus pubens*, c = *Viburnum cordifolium*, sy = *Symphoricarpos albus*, t = *Triosteum aurantiacum*.

(P) of pollen in this class is 24.4 μm ($s = 4.719$), the mean width (E) is 20.4 μm ($s = 2.995$), and the mean P/E quotient is 1.23 (subprolate).

Pollen in size-shape class II ranges from 26.8 (*Symphoricarpos albus*) to 56.4 μm long (*Triosteum aurantiacum*), and from 30.9 (*S. albus*) to 64.1 μm wide (*T. aurantiacum*). The mean length (P) of pollen in this class is 43.6 μm ($s = 8.481$), the mean width (E) is 47.4 μm ($s = 8.942$), and the mean P/E quotient is 0.91 (oblate spheroidal).

Those species for which size data were not obtained have been tentatively assigned to one of the two size-shape classes based on visual comparisons with

pollen of known size. There is little chance of misclassification because the two classes are nonoverlapping and readily contrasted.

EXINE STRUCTURE-SCULPTURE CLASSES. There is great diversity in exine structure and sculpture within the *Caprifoliaceae s.l.*, and to a lesser extent within *Viburnum*. The pollen of each species was assigned to one of six exine structure-sculpture classes described below. Within some of the classes there is considerable variation, and they may be subdivided as SEM studies are extended and augmented by LM and TEM investigations.

Class a. Exine semitectate, \pm regularly reticulate; reticulum elevated on columellae (height variable both within and between grains); muri psilate, variable in width; lumen dimensions variable; free-standing bacula and/or pila present, generally visible in lumina, variable in size and number (e.g., PLATE I).

Class b. Exine semitectate, \pm regularly reticulate; reticulum \pm elevated on columellae (these sometimes laterally continuous); muri regularly scabrate; lumen dimensions variable; bacula present and visible in lumina, variable in size and number but often smaller and less abundant than in class a (e.g., PLATE VI).

Class c. Exine intectate or with some fusion of heads of adjacent pila, \pm regularly retipilate (Erdtman, 1966) to pilate; pila short stalked or nearly sessile (gemmae), scabrate (except in *Viburnum cordifolium*; see PLATE VE, F, and discussion); distinct lumina absent; surfaces between pila verrucate to irregularly baculate (e.g., PLATE VII).

Class d. Exine tectate, imperforate, bearing spinelike processes (echinae $\geq 1 \mu\text{m}$, microechinae $< 1 \mu\text{m}$) of variable size and abundance; surfaces between spines psilate to verrucate; tectum supported by columellae of variable height and width (e.g., PLATES XD-F, XIA-D).

Class e. Similar to class d, except lacking spinelike processes on tectum (e.g., PLATE XA-C).

Class f. Exine lacking columellae; tectum bearing large, often irregularly shaped spinelike processes; surface between spines \pm verrucate (e.g., PLATE IXC-F).

These exine structure-sculpture classes fall into two categories. The first includes classes a-c, in which the exine is semitectate and reticulate to intectate. The second comprises classes d-f, which are characterized by a complete tectum, either raised on columellae (d and e) or not (f).

POLLEN TYPES. Together, size-shape class and structure-sculpture class define a pollen type. Structure-sculpture classes a-c occur only in pollen grains in size-shape class I, while the structure-sculpture classes d-f are found only in grains of size-shape class II (FIGURE 1). Hence, there are two very different kinds of pollen grains in the *Caprifoliaceae s.l.*: those that are smaller, prolate, and lacking a complete tectum; and those that are larger, oblate to spheroidal, and completely tectate.

APERTURE MORPHOLOGY AND POLLEN TYPES. Since variation in aperture morphology was not analyzed in detail in this study and has not received sufficient attention previously, aperture differences were not included in the descriptions of pollen types given above. Only the SEM was employed in this survey; careful

studies with the LM and TEM are necessary to understand the nature and extent of variation in aperture structure. However, some general observations about aperture morphology in the Caprifoliaceae *s.l.* can be made, and it is possible to relate what little is known about aperture variation to variation in the characters discussed above. These comments are based in part on the LM studies of Bassett and Crompton (1970), Richard (1970), Punt and colleagues (1974), and Böhnke-Gütlein and Weberling (1981).

Pollen of all members of the Caprifoliaceae *s.l.* is normally triaperturate, with an occasional two- to four-apertured grain (e.g., in some specimens of *Abelia spathulata*, PLATE XIC). The apertures are distinctly colpiate in *Viburnum*, *Sambucus*, and *Adoxa*, and brevicolporate to porate in the Caprifoliaceae *s.s.* Thus, the taxonomic distribution of aperture shapes seems to correlate perfectly with the distributions of the size, shape, and exine characters just described (see below).

Minor variations in aperture structure have been reported in *Viburnum*, and some of these may prove taxonomically useful. Presently, however, the nature of this variation is very poorly known. For example, Bassett and Crompton (1970) noted variation in the extent to which the furrows appeared open. Unfortunately, this trait appears to vary within some species and may be affected by the method of preparation. A somewhat more promising character is the presence or absence of a bridge over the colpus, a feature recorded both by Punt and colleagues (1974) and by Böhnke-Gütlein and Weberling (1981). In their combined sample of 31 species, a bridge was present in 15, including all 6 species examined with an exine of type b or c. Variation in this trait is apparently common within several sections (e.g., ODONTOTINUS) and in some cases might be useful in distinguishing between closely related species. However, this character should be treated very cautiously until it is studied in more detail because there are several conflicting observations. In *V. tinus*, for example, Böhnke-Gütlein and Weberling (1981) reported the presence of a bridge, while Punt and co-workers (1974) recorded its absence. The latter observation is supported in the present study (PLATE IIIC). Other similar conflicts, and the observation of apparently intermediate conditions in some grains, suggest that there can be considerable variation within species and/or that this trait can be affected by sample preparation.

Within the Caprifoliaceae *s.s.* there appear to be slight but consistent differences in aperture shape between the genera. In *Heptacodium* (PLATE VIIIF), *Diervilla* (PLATE IXC), *Weigela* (PLATE IXE), and *Triosteum* (PLATE XA, B) the apertures are porate or only slightly elongate, while in the remaining genera they are usually brevicolporate. However, in *Symphoricarpos* the apertures reportedly vary (Bassett & Crompton, 1970), and they may be intermediate in length (PLATE XC). Obviously, many more species will have to be examined before this character can be used with any confidence.

POLLEN TYPES AND PHYLOGENETIC RELATIONSHIPS IN THE CAPRIFOLIACEAE *S.L.*

The taxonomic distribution of pollen types within the Caprifoliaceae *s.l.* is quite clear cut. Type Ia grains characterize *Sambucus*, *Adoxa*, and most species of *Viburnum*; types Ib and Ic are also found in *Viburnum*. Type IId is most

common in the Caprifoliaceae *s.s.*, but IIe and II f are also present. Thus, pollen types are congruent with many other characters that suggest the presence of two distinct lineages within the Caprifoliaceae *s.l.* (Donoghue, 1983b). It is noteworthy that pollen size appears to be positively correlated with style length. This supports the conclusions of Plitmann and Levin (1983), who studied pollen-pistil relationships in Polemoniaceae. Style length is in turn correlated with other floral characters (e.g., length of corolla tube) that relate to mode of pollination.

A cladistic analysis aimed at determining the phylogenetic relationships of *Viburnum* (Donoghue, 1983b) demonstrated that there are shared derived character states (synapomorphies) uniting *Viburnum* with *Sambucus* and *Adoxa* almost regardless of what outgroup arrangement is used in assessing character polarities. The ten genera of Caprifoliaceae *s.s.* may form a monophyletic group, but they are probably paraphyletic (i.e., would not include all of the descendants of their common ancestor) if the Valerianaceae and Dipsacaceae are treated as separate families. There is no evidence that the Caprifoliaceae *s.l.* are a monophyletic group (I have been unable to find a synapomorphy linking *Viburnum*, *Sambucus*, and *Adoxa* with the Caprifoliaceae *s.s.*).

Since there is no reason to think that the Caprifoliaceae *s.l.* form a monophyletic group, it is inappropriate to consider the evolution of pollen morphology in the group as a whole, as has been done in previous studies (e.g., Böhnke-Gütlein & Weberling, 1981). Therefore, I will consider pollen evolution only within the two distinct groups of Caprifoliaceae *s.l.*, especially within the *Viburnum-Sambucus-Adoxa* clade, for which there exists a corroborated hypothesis of phylogenetic relationship. Thus I will consider transformations between pollen types Ia, Ib, and Ic, and between types II d, II e, and II f, but I will not treat relationships between the two main pollen types because a direct transformation between them may never have occurred.

EVOLUTION OF THE EXINE

EXINE EVOLUTION IN VIBURNUM

TAXONOMIC DISTRIBUTION OF EXINE CHARACTERS. Only type Ia pollen is known in *Sambucus* and *Adoxa*, and this type predominates in *Viburnum*. There do appear to be slight variations in pollen type Ia between the genera. On average, the lumina in *Sambucus* and *Adoxa* are smaller than those in *Viburnum*, and therefore the reticulum appears to be tighter (Plate VIII A-D). Pollen of *Sambucus* and *Adoxa* is also somewhat smaller on average than that of most species of *Viburnum*. More free columellae are visible within the lumina of *Viburnum* and *Sambucus* than in those of *Adoxa*. Each of these differences is slight, and there is considerable overlap. Thus, without additional study of a larger sample, they cannot be considered statistically or taxonomically significant.

Type Ia pollen not only is the most common one in *Viburnum* but is also taxonomically widespread. Rehder (1908, 1940) recognized nine sections in the genus. These are widely accepted but have been subdivided in a few cases (e.g., Kern, 1951). Hara (1983) provided an overview of the subgeneric clas-

sification and modified Rehder's classification, recognizing 10 sections; he placed the Latin American species (Killip & Smith, 1931; Morton, 1933) in sect. OREINOTINUS. In TABLE 1 the species of *Viburnum* examined in this study are arranged according to Hara's sections. The table shows that type Ia pollen is present in all examined members of sects. ODONTOTINUS (PLATE IA-D), OREINOTINUS (PLATE IE, F), SOLENOTINUS (PLATES IIA-F; IIIA, B), TINUS (PLATE IIIC-F), TOMENTOSA (PLATE IVE, F), and OPULUS (PLATE VA, B), as well as in *V. cylindricum* of sect. MEGALOTINUS (PLATE IVA, B), *V. urceolatum* of sect. VIBURNUM (PLATE IVC, D), and *V. furcatum* (PLATE VC, D) and *V. lantanoides* of sect. PSEUDOTINUS. Type Ia pollen is not known in sect. LENTAGO.

There is some variation in pollen type Ia within *Viburnum*; upon additional study of a larger sample, this is likely to be of some taxonomic significance within sections and species complexes. Variation in the size of the lumina and in the abundance and visibility of bacula is especially pronounced in sect. SOLENOTINUS (formerly *Thyrsosma* (Raf.) Rehder), which contains 15 to 20 species native to Asia. In *V. farreri* (subsect. LONICEROIDES (Oersted) Hara; PLATE IIA) the lumina are narrow and the bacula are hardly visible. In contrast, in *V. erubescens*, *V. oliganthum*, and *V. suspensum* (all subsect. SOLENOTINUS), and in *V. odoratissimum* (subsect. MICROTINUS (Oersted) Hara; PLATE IIE, F), the reticulum is loose and conspicuously raised. In *V. brachybotryum* (subsect. MICROTINUS; PLATE IIIA, B) the lumina are especially wide and numerous bacula are visible.

Section SOLENOTINUS is generally believed to include the most primitive species in *Viburnum* (Wilkinson, 1948; DeVos, 1951; Egolf, 1962; Hara, 1983), and it may be paraphyletic (Donoghue, 1983a). Since there is extreme diversity within the section in leaf venation, margin, size, and shape, and in flowering time, fruit morphology, and growth pattern (Donoghue, 1982, 1983a; Hara, 1983), the range of variation in pollen morphology is not altogether surprising. It is noteworthy that the minor variations in pollen noted above do seem to distinguish some of Hara's subsections, suggesting that these may be natural groups.

Some of the range of variation in sect. SOLENOTINUS is paralleled in sect. TINUS, a monophyletic group of approximately eight species. The pollen of *Viburnum atrocyaneum* (PLATE IIIF) is similar to that of *V. odoratissimum* (PLATE IIE, F), and *V. tinus* pollen (PLATE IIIC, D) is like that of *V. brachybotryum* (PLATE IIIA, B). Pollen of *V. cinnamomifolium*, *V. davidii* (PLATE IIIE), and *V. propinquum*, all of which have trinerved leaves (i.e., acrodromous venation), does not appear to differ significantly from that of the remaining species of sect. TINUS, which have pinnate (eucamptodromous) venation.

Compared to pollen type Ia, types Ib and Ic are much less common and more limited in taxonomic distribution. Type Ib characterizes *Viburnum punctatum* of sect. MEGALOTINUS subsect. PUNCTATA Kern (PLATE VIE, F) and four of the ten species examined from sect. VIBURNUM. Section VIBURNUM, with 15 to 20 species, is divided by Hara (1983) into three subsections: subsect. VIBURNUM has pollen types Ib and Ic; *V. carlesii*, the only species of subsect. SOLENOLANTANA (Nakai) Hara, has type Ib; and *V. urceolatum* of the monotypic

subject. URCEOLATA Nakai has type Ia. The last species may not be closely related to the others (see below and Donoghue, 1983a). Species of sect. VIBURNUM with types Ib and Ic pollen have never been placed in separate groups. Type Ib pollen is also known from sect. LENTAGO but is extremely rare in this group; it was found in only one out of the four individuals of *V. nudum* var. *cassinoides* examined.

Pollen type Ic characterizes the majority of the examined species of sects. VIBURNUM (PLATE VIID-F) and LENTAGO. *Viburnum cordifolium* (PLATE VE, F) of sect. PSEUDOTINUS was also initially scored as having type Ic pollen, but as noted above, the pila in this species appear to lack scabrae. The analysis below indicates that this kind of pollen is best considered a distinct type.

There are some differences in grain shape in groups with pollen types Ib and Ic, and these may prove taxonomically useful when examined in more detail. Most *Viburnum* species have prolate or subprolate grains, but there is a trend toward spheroidal or oblate ones, especially in sect. VIBURNUM (PLATES VIC, D; VIID, E). The bearing of this observation on the interpretation of exine evolution is considered below.

POLARITY AND TRANSFORMATION SERIES. Only shared derived character states (synapomorphies) may be considered evidence of common ancestry; within a particular group shared ancestral states (symplesiomorphies) are uninformative about cladistic relationship (Hennig, 1966). Hence, before the *Viburnum* pollen data assembled here can be used to assess phylogenetic relationships, the polarity of the exine characters must be determined. Numerous criteria have been used to assess polarity, but outgroup comparison is now widely acknowledged to be the only generally valid one (Stevens, 1980, 1981; Watrous & Wheeler, 1981; Wheeler, 1981; Farris, 1982; Maddison *et al.*, 1984).

Elsewhere (Donoghue, 1983b), I have defended the hypothesis that *Sambucus* and *Adoxa* together are the sister group of *Viburnum*. *Sambucus* and *Adoxa* can therefore be used as an outgroup to assess the polarity of characters that vary in *Viburnum*. If *Sambucus* and *Adoxa* share a state that occurs in some members of *Viburnum*, then it is most parsimonious to consider that state to be ancestral within *Viburnum*, and the alternate state(s) to be derived (Maddison *et al.*, 1984). Thus pollen type Ia can be considered the ancestral state in *Viburnum*, and types Ib and Ic derived.

It would be desirable to include outgroups in addition to *Sambucus* and *Adoxa* in the analysis of polarity (Maddison *et al.*, 1984), but the sister group of the *Viburnum-Sambucus-Adoxa* clade is equivocal. In cases such as this, plausible sister groups can usually be substituted to see what effect they might have on polarity assessment (Donoghue & Cantino, 1984), but in this instance all plausible sister groups are highly variable in pollen morphology and/or homologies are difficult to establish. The Cornaceae, for example, are a likely secondary outgroup but are quite variable, and intrafamilial relationships are so poorly understood that the family cannot be employed in outgroup comparison. Chao (1954) noted that pollen of the Cornaceae resembles that of *Viburnum*, *Sambucus*, and *Adoxa* in size, shape, and aperture number and morphology. Ferguson (1977) revealed a wide variety of pollen types in the

Cornaceae, none of which is identical to pollen of *Viburnum*, *Sambucus*, or *Adoxa*. It is noteworthy, however, that species of *Melanophylla* Baker have pollen similar to type Ia; *Kaliphora madagascarensis* Hooker f. pollen resembles type Ib; and *Aucuba japonica* Thunb. pollen is similar to type Ic. Derivation of the *Viburnum-Sambucus-Adoxa* clade from ancestors similar to extant Cornaceae would not have required major changes in pollen morphology but would necessitate a transformation to the trinucleate condition from the binucleate state characteristic of the Cornales (Brewbaker, 1967).

By outgroup comparison it is possible to establish the most parsimonious hypothesis of ancestral state in the ingroup. For two-state (binary) characters, the derived state and its relation to the ancestral state are automatically determined. When there are three or more states, a transformation series must be established, specifying the relation among the states. There have been attempts to develop rigorous methods to establish transformation series (Mickevich, 1982), but this requires that other characters be examined simultaneously and that an initial hypothesis of cladistic relationships be formulated. In the absence of such information, transformation series have been constructed on the basis of the "logical" relations among the states and/or by reference to general trends in similar organisms (Stevens, 1980). Fortunately, in the case of the exine characters considered here, it is possible to use parsimony as a criterion to choose among the possible transformation series because the exine structure-sculpture classes involve two independently varying characters (scabrae present or absent; regular reticulum present or absent). Furthermore, these characters are nested such that retipilate or pilate grains are scabrate (except in *Viburnum cordifolium*), but some grains with scabrae are reticulate. For these reasons it is most parsimonious to posit that Ia → Ib → Ic (FIGURE 2A). This transformation series requires two state changes: from smooth to scabrate, and from reticulate to retipilate/pilate. Any other arrangement of pollen types (Ia → Ic → Ib, or Ib ← Ia → Ic) requires a minimum of three steps. The most parsimonious transformation series is consistent with a supposedly common trend from semitectate and reticulate to intectate pollen (Walker & Doyle, 1975; Walker, 1976).

In contrast, Böhne-Gütlein and Weberling (1981) concluded that Ic → Ib → Ia, based on unsubstantiated preconceptions about phylogenetic relationships and the relative advancement of species within *Viburnum*, and on a presumed trend (Erdtman, 1966) from pilate to reticulate grains. This conclusion is rejected here based on outgroup comparison. A phylogenetic analysis of relationships within *Viburnum* (see below and Donoghue, 1983a) also shows that it is most parsimonious to hypothesize that Ia is ancestral in *Viburnum*.

CLADISTIC RELATIONSHIPS AND EXINE EVOLUTION. If pollen type Ia is ancestral within *Viburnum*, possession of this trait does not provide evidence of cladistic relationship within the genus. Types Ib and Ic are derived and provide *prima facie* evidence of monophyly. The simplest hypothesis, based on the transformation series established above, is that type Ib evolved once and characterizes a monophyletic group, and that type Ic likewise evolved from Ib only once (FIGURE 2B). To test this hypothesis and establish the level at which these

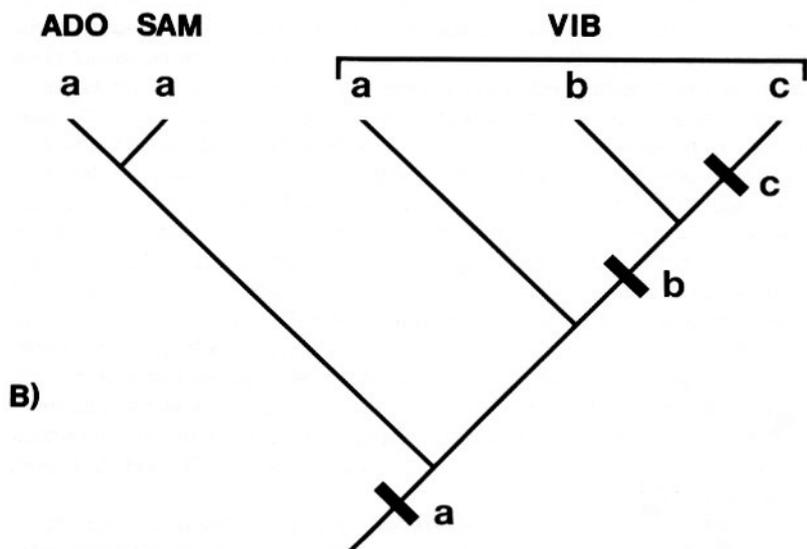
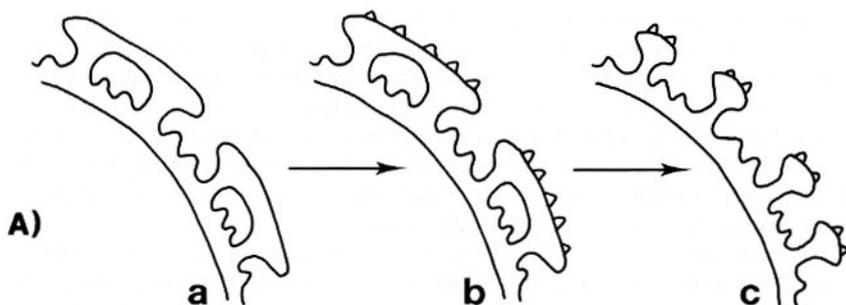


FIGURE 2. A, hypothesized transformation of pollen structure-sculpture classes a, b, and c within *Viburnum* (all size-shape class I). B, simplest *a priori* phylogenetic hypothesis for evolution of pollen in *Viburnum* (VIB), with *Sambucus* (SAM) and *Adoxa* (ADO) as first outgroup.

states characterize monophyletic groups, it is necessary to consider the congruence of the pollen characters with other characters. Such congruence will test whether plants with type Ic pollen, for example, form a monophyletic group, and hence whether Ic is truly a homology (Patterson, 1982). In practice the congruence test of homology is performed by using a variety of characters to construct the most parsimonious cladogram.

In a preliminary cladistic analysis of *Viburnum*, I used a data set of 23 species

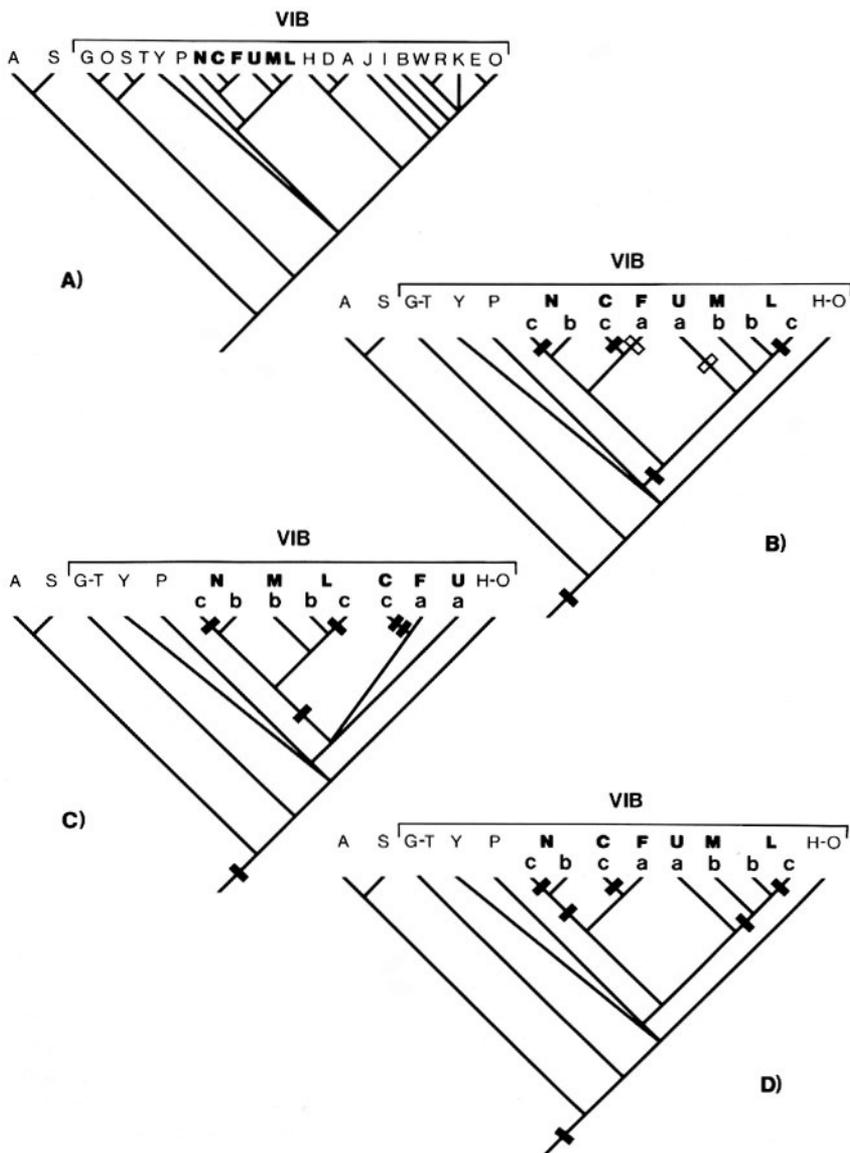


FIGURE 3. A, cladogram of *Viburnum* (VIB) used in evaluating pollen evolution; *Sambucus* (S) and *Adoxa* (A) as first outgroup. Clade N, C, F, U, M, L (boldface) expanded in B–D. B, most parsimonious interpretation of pollen evolution using transformation series in FIGURE 2A (black bar = forward transformation; open bar = reversal; a, b, c = structure-sculpture classes of size-shape class I). C, rearrangement of cladogram A, eliminating reversals in the pollen character but entailing extra steps in other characters. D, most parsimonious arrangement of character-state transformations on cladogram A after reinterpretation of homologies.

complexes scored for 34 characters involving buds, leaves, branching patterns, trichomes, inflorescences, flowers, and fruits (Coombs *et al.*, 1981; Donoghue, 1983a). Exine morphology was one character in the analysis: the states were pollen types Ia, Ib, and Ic; polarity and transformation series were assessed as discussed above. Cladograms were constructed using the WAGNER '78 computer program, which searches for the arrangement of taxa that minimizes the total number of character state changes, allowing both forward and reverse transitions (Farris, 1970). Several cladograms were generated because some characters exhibiting the most homoplasy, and about which there was the most uncertainty, were removed. The cladogram obtained using 28 characters (see FIGURE 3A) will serve as the basis for discussing exine evolution. The general conclusions below would not change substantially if any of the other cladograms shown in Donoghue (1983a) were used, because most of the changes in the exine occur within "stable clades" that remained unchanged on all cladograms or, more often, within the terminal taxa used in the analysis.

Detailed information about the cladistic analysis of *Viburnum* is given in Donoghue (1983a). It is important to note that each letter in FIGURE 3 symbolizes a species or a species complex, each of which is thought to be monophyletic. Of particular importance for this discussion, sect. MEGALOTINUS was split into *V. cylindricum* (Y) and subsect. PUNCTATA (M); *V. urceolatum* (U) was removed from sect. VIBURNUM (N); and *V. cordifolium* (C) was treated as distinct from *V. lantanoides* and *V. furcatum* of sect. PSEUDOTINUS (F). Section LENTAGO is symbolized by L.

On the cladogram in FIGURE 3A, pollen character-state changes occur only within the clade comprising taxa N through L; therefore, in FIGURE 3B-D this clade is enlarged while others are represented by single lines. On this cladogram it is most parsimonious to hypothesize that Ib pollen arose once in the common ancestor of *Viburnum urceolatum*, *V. cordifolium*, and sects. VIBURNUM, LENTAGO, PSEUDOTINUS, and MEGALOTINUS subsect. PUNCTATA (FIGURE 3B). However, the arrangement of these taxa in the cladogram requires reversals to type Ia pollen in *V. urceolatum* (U) and in sect. PSEUDOTINUS (F). In addition, according to this hypothesis, pollen type Ic must have been derived independently from type Ib in *V. cordifolium* (C) and within sects. VIBURNUM (N) and LENTAGO (L).

If this cladogram of *Viburnum* is substantially correct, there must have been reversals and parallelisms in the pollen character. However, the relatively small change in the cladogram of FIGURE 3A shown in FIGURE 3C makes it possible to do away with reversals from Ib to Ia that palynologists may consider to be unlikely. In this cladogram sect. VIBURNUM (N) is linked with sects. LENTAGO (L) and MEGALOTINUS subsect. PUNCTATA (M), and taxa C, F, and U are excluded. Such a change would, of course, entail some additional steps overall. However, many more steps would be necessary to eliminate the need to postulate the independent origin of Ic pollen; in particular, one would have to assume that C, L, and N were a clade within which sects. LENTAGO and VIBURNUM were not monophyletic. This is very unparsimonious because there is strong support from other characters for the linkage of C with F and of L with M, and for the monophyly of the terminal taxa, especially L (Donoghue, 1983a).

From the foregoing it seems that pollen type Ib may be a homology but that type Ic is very probably not, having arisen three separate times. The hypothesis that type Ic is not a homology leads to the question of whether the exact same morphology evolved three times, or whether there are morphological differences that corroborate the hypothesis of convergence. Comparison of type Ic pollen in sect. *LENTAGO* with that in sect. *VIBURNUM* reveals a rather consistent difference in shape (see FIGURE 1): grains in sect. *LENTAGO* are subprolate or more often euprolate, while both Ib and Ic pollen in sect. *VIBURNUM* (excepting *V. mongolicum*) is spheroidal or oblate (e.g., compare PLATE VIIA to VIID, E). This difference in shape between the groups lends support to the hypothesis of convergence suggested by the cladogram.

On reexamination *Viburnum cordifolium* pollen was found to lack scabrae on the pila, unlike type Ic pollen in sects. *LENTAGO* and *VIBURNUM*. This distinction, also noted by Böhnke-Gütlein and Weberling (1981), supports the hypothesis that the pilate exine of *V. cordifolium* was achieved independently. Because *V. lantanoides* and *V. furcatum* (both with type Ia pollen) are the sister group of *V. cordifolium* in FIGURE 3A, it may be that *V. cordifolium* pollen evolved directly from type Ia. This interpretation is more parsimonious than one that postulates a derivation through type Ib, which would require both the gain and loss of scabrae.

These observations suggest the alternative explanation of pollen character-state transformations, shown in FIGURE 3D. According to this interpretation, relationships remain the same as in the original cladogram (FIGURE 3A, B), but there are two origins of type Ib—one in the ancestor of N (oblate grains) and the other in the ancestor of M plus L (prolate grains). Type Ic has then evolved independently within each of these groups. *Viburnum cordifolium* pollen is considered to have evolved directly from type Ia. This hypothesis entails no reversals and requires a total of five state changes—one less than in FIGURE 3B.

In future cladistic analyses of *Viburnum*, pollen characters should be recoded to reflect the understanding of homologies obtained from the first cladograms. Indeed, it is now evident that pollen variation involves at least three characters that can vary independently: presence or absence of a reticulum, presence or absence of scabrae, and shape of the grain.

EXINE EVOLUTION IN CAPRIFOLIACEAE S.S.

TAXONOMIC DISTRIBUTION OF EXINE CHARACTERS. All species of the Caprifoliaceae s.s. examined have pollen in size-shape class II, but there is considerable variation in grain size (see FIGURE 1). With further study of a larger sample, this variation may prove taxonomically significant. However, size differences do not appear to be correlated with differences in exine structure and sculpture, nor do they correspond to the standard tribal classification of the group. Bassett and Crompton (1970) noted that variation in grain size within *Symphoricarpos* was correlated with chromosome number. The size reported here for *S. albus* is close to that reported for tetraploid individuals; octaploids are said to have larger grains.

The most significant pollen difference within the Caprifoliaceae *s.s.* is in exine structure. In tribes Caprifolieae, Triosteae, and Linnaeae the complete tectum is raised on columellae of various sizes (pollen types IId and IIe, PLATES IXA, B; XB, D; XID). In contrast, in *Diervilla* and *Weigela* (tribe Diervilleae) columellae appear to be lacking (pollen type II_f, PLATE IXF).

The sculpturing of the exine also varies. In all species of tribes Caprifolieae and Diervilleae and most species of tribe Linnaeae examined, spines are present. These processes vary somewhat in shape, size, and abundance. The two species of *Triosteum* (Triosteae) and the single species of *Symphoricarpos* (Linnaeae) examined differ in lacking supratectal spines; instead the tectum is psilate or fossulate (pollen type IIe, PLATE XA-C).

POLARITY AND TRANSFORMATION SERIES. Since there is no well-corroborated hypothesis of the broader cladistic relationships of the Caprifoliaceae *s.s.*, it is difficult to employ outgroup comparison to assess polarity. Indeed, as noted above, it is not clear that the Caprifoliaceae *s.s.* constitute a monophyletic group. If both the Dipsacales (excluding *Viburnum*, *Sambucus*, and *Adoxa*) and the Caprifoliaceae *s.s.* were assumed to be monophyletic, then the Valerianaceae and the Dipsacaceae could be used as outgroups to assess polarities in the Caprifoliaceae *s.s.* The pollen of the Valerianaceae (e.g., PLATE XIE, F) and the Dipsacaceae is most like type IId (Clarke & Jones, 1977; Patel & Skvarla, 1979), which could therefore be considered ancestral in the Caprifoliaceae *s.s.* There are, however, some noteworthy differences between the pollen of these families. In particular, spines of various kinds are associated with the apertures in the Valerianaceae (Patel & Skvarla, 1979; PLATE XIE) and the Dipsacaceae.

Since many botanists (e.g., Wilkinson, 1949) believe that the Valerianaceae and the Dipsacaceae are derived from tribe Linnaeae of the Caprifoliaceae *s.s.* through an ancestor similar to the extant genus *Nardostachys* DC. of the Valerianaceae, these two families may not be an appropriate outgroup. Even if the Caprifoliaceae *s.s.* were paraphyletic, pollen type IId might still be the ancestral condition in the Dipsacales, retained and modified in the evolution of the Valerianaceae and the Dipsacaceae.

The Rubiaceae are often considered to be closely related or even ancestral to the Caprifoliaceae (e.g., Cronquist, 1968, 1981). Pollen morphology is extremely variable within Rubiaceae (Erdtman, 1966), and without a better understanding of phylogenetic relationships within this family one cannot use it as an outgroup for the Caprifoliaceae *s.s.*

Lacking an outgroup, it would be possible to assess polarity tentatively if cladistic relationships were known within the Caprifoliaceae *s.s.* Although a cladistic analysis has not been performed, it is widely believed that tribe Caprifolieae (especially *Leycesteria*) is the most primitive group, from which the other three tribes have been derived (e.g., Wilkinson, 1949). Since all Caprifolieae have type IId pollen, this might provisionally be considered the ancestral state, with types IIe and II_f derived.

If type IId is considered ancestral based on the circumstantial reasoning above, how are the derived types IIe and II_f related to it—i.e., what is the transformation series? Two binary characters are involved in defining these exine types: presence or absence of columellae, and presence or absence of

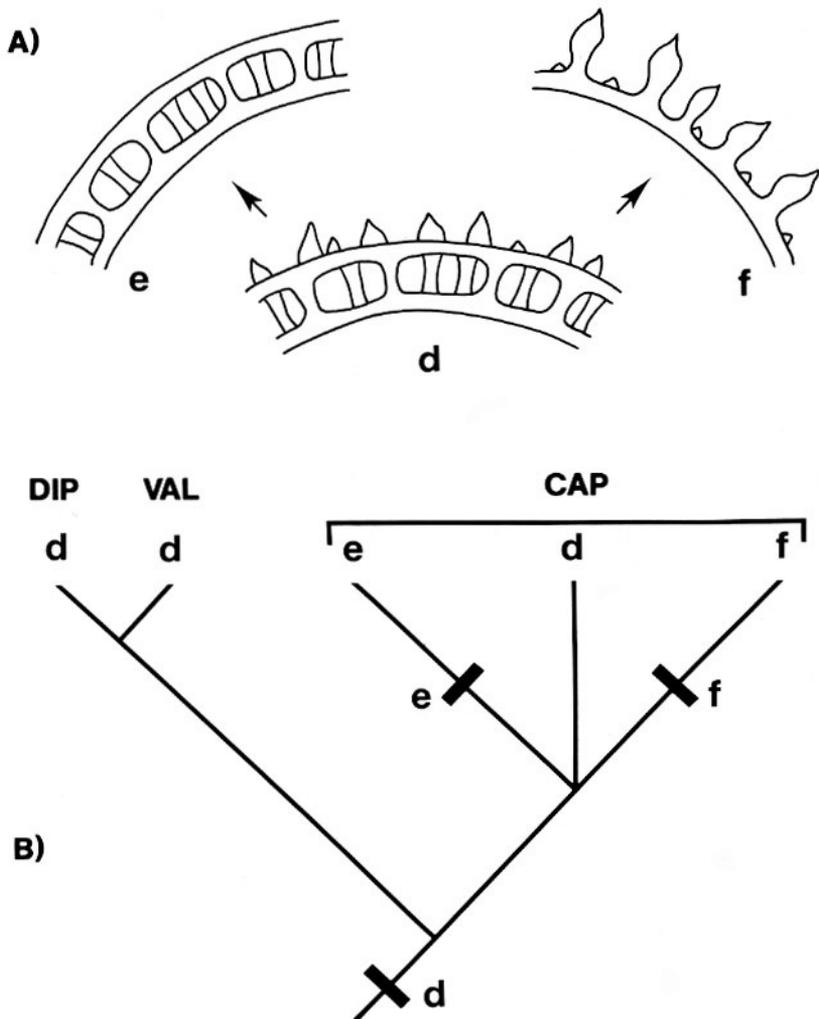


FIGURE 4. A, hypothesized transformation of pollen structure-sculpture classes d, e, and f within Caprifoliaceae s.s. (all size-shape class II). B, simplest *a priori* phylogenetic hypothesis for evolution of pollen in Caprifoliaceae s.s. (CAP), with Valerianaceae (VAL) and Dipsacaceae (DIP) as first outgroup.

supratectal spines. As in the case of *Viburnum*, *Sambucus*, and *Adoxa* discussed above, it is possible to choose from among possible transformation series based on parsimony. In this instance it is most parsimonious to assume that IIe and II f are independently derived from II d (FIGURE 4A). Any other arrangement requires at least one additional step.

The derivation of type IIe from II d simply entails the loss of spines on the tectum. The most parsimonious explanation for the derivation of type II f is

that the columellae were lost, with the tectum therefore resting on the foot layer. An alternative explanation requires the loss of both the tectum surrounding the spines and the columellae not directly subtending spines. If this were the case, the spines in tribe Diervilleae would be derived in part from columellae and in part from tectum and suprategal spines. There is currently no evidence to support this more complicated explanation, but TEM studies might be useful.

CLADISTIC RELATIONSHIPS AND EXINE EVOLUTION. If pollen type II_d is considered ancestral, then only possession of types II_e or II_f can provide evidence of monophyly. The simplest hypothesis would be that both II_e and II_f evolved only once (FIGURE 4B). If this is so, then type II_f indicates that tribe Diervilleae is monophyletic, which is corroborated by several other unique features (notably the elongate bilocular ovary that develops into a many-seeded capsule).

Pollen type II_e suggests that *Triosteum* and *Symphoricarpos* form a monophyletic group. *Triosteum* has previously been allied with *Viburnum* (Fritsch, 1891; Wagenitz, 1964) or has been placed in its own tribe, but Lewis and Fantz (1973) concluded that it is most similar to *Lonicera*. *Symphoricarpos* is generally considered the basal member of tribe Linnaeae (Wilkinson, 1949). A phenetic analysis (Hsu, 1983) showed that *Triosteum* and *Symphoricarpos* have much in common, but to my knowledge, a direct phylogenetic relationship between them has never been defended. It is noteworthy that both genera have dry or mealy drupes with several one-seeded endocarps, and that the seedlings and sucker shoots of *Symphoricarpos* often have lobed leaves similar to those of *Triosteum*. On the other hand, the possibility that pollen type II_e arose independently in the two genera is suggested by a marked difference in pollen size. *Triosteum* has the largest and *Symphoricarpos* the smallest grains of any members of the Caprifoliaceae *s.s.* examined (TABLE 2, FIGURE 1). Determining whether II_e is a homology or if there has been convergence will require a detailed phylogenetic analysis of the Caprifoliaceae *s.s.*

SUMMARY

Although the pollen of the Caprifoliaceae *s.l.* is now very well known, the evolution of pollen diversity has not been considered in detail and the phylogenetic significance of pollen characters is not widely appreciated. This study confirms that there are major differences in pollen size and shape, as well as significant variation in exine structure and sculpturing, in the Caprifoliaceae *s.l.* These variables define two very different kinds of pollen: the large, oblate, tectate grains of the Caprifoliaceae *s.s.*, and the small, usually prolate, semi-tectate ones of *Viburnum*, *Sambucus*, and *Adoxa*. This distribution of pollen types is consistent with the idea that the Caprifoliaceae *s.l.* are divisible into two distinct lineages and do not constitute a monophyletic group. It may therefore be inappropriate to consider the evolution of pollen morphology in the Caprifoliaceae *s.l.* as a whole because there may never have been a direct evolutionary transition between the two main pollen types within the group. However, it is appropriate to consider pollen evolution within each of the two

component lineages, especially within the clade comprising *Viburnum*, *Sambucus*, and *Adoxa*.

Previous discussions of pollen evolution in the Caprifoliaceae *s.l.* (and in most other groups) have been based upon generally accepted but mostly untested ideas about which groups are relatively primitive and which ones advanced, and upon presumably general trends. In the present analysis pollen evolution is considered in the context of explicitly cladistic hypotheses for the groups involved. Polarity of pollen characters is assessed by outgroup comparison, and the most parsimonious transformation series is established. In *Viburnum* semitectate, reticulate grains with smooth muri appear to represent the ancestral condition; the addition of scabrae and the breakdown of the reticulum are derived. When exine characters are used along with others, a cladogram is obtained that may require reversals but quite certainly necessitates the independent evolution of retipilate or pilate grains in three separate groups. Upon reexamination of the pollen in these three groups, slight but consistent differences are found that corroborate the hypothesis of convergence and suggest a more parsimonious interpretation of pollen evolution. The retipilate/pilate condition should not be considered a homology, and pollen characters should be recoded in subsequent phylogenetic analyses of *Viburnum*.

A detailed analysis of pollen evolution in the Caprifoliaceae *s.s.* is not possible at this time because this group may not be monophyletic, its outgroups are equivocal, and a hypothesis of cladistic relationships within the group is not yet available. Circumstantial evidence suggests, however, that grains with the tectum raised on columellae and with supracteal spines are probably ancestral. Spines are lacking in *Symphoricarpos* and *Triosteum*, which may indicate a sister-group relationship between these genera. The absence of columellae in the Diervilleae corroborates the monophyly of this tribe.

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EXPLANATION OF PLATES

PLATE I

Pollen of *Viburnum* sects. ODONTOTINUS (A–D) and OREINOTINUS (E, F): A, *V. foetidum* (Forrest 18129, A); B, *V. dilatatum* (Ohashi, Nakaike, & Tateishi 70627, A); C, *V. japonicum* (Ichikawa 26, A); D, *V. wrightii* (Hatusima 4206, A); E, F, *V. microcarpum* (Ventura A. 819, ENCB); all type Ia. Scale bars = 10 μ m (A–C, E) or 1 μ m (D, F).

PLATE II

Pollen of *Viburnum* sect. SOLENOTINUS: A, *V. farreri* (Rock 12142, A); B, *V. suspensum* (Hatusima 864, GH); C, *V. oliganthum* (H. Smith 1961, A); E, *V. odoratissimum* (Alcasid 70, A); F, *V. odoratissimum* (H. H. Hu 770, A); all type Ia. Scale bars = 10 μ m (A–E) or 1 μ m (F).

PLATE III

Pollen of *Viburnum* sects. SOLENOTINUS (A, B) and TINUS (C–F): A, B, *V. brachybotryum* 12790A, A); C, D, *V. tinus* (Marchesetti 2752, GH); E, *V. davidii* (Wilson 3728, A); F, *V. atrocyaneum* (Rock 8905, A); all type Ia. Scale bars = 10 μ m (A, C, E, F) or 1 μ m (B, D).

PLATE IV

Pollen of *Viburnum* sects. MEGALOTINUS (A, B), VIBURNUM (C, D), and TOMENTOSA (E, F): A, B, *V. cylindricum* (Iwatsuki, Koyama, Fukuoka, & Nalampoon 9424, A); C, D, *V. urceolatum* (Tashiro s.n., 1917, A); E, F, *V. hanceanum* (Chun 5314, A); all type Ia. Scale bars = 10 μ m (A, C, E) or 1 μ m (B, D, F).

PLATE V

Pollen of *Viburnum* sects. OPULUS (A, B) and PSEUDOTINUS (C–F): A, *V. sargentii* (Furuse s.n., 20 June 1961, A); B, *V. sargentii* (Furuse s.n., 9 June 1958, A); C, D, *V. furcatum* (Togashi 7145, A); E, F, *V. cordifolium* (Forrest 11892, A). A–D, type Ia; E, F, type Ic. Scale bars = 10 μ m (A–C, E) or 1 μ m (D, F).

PLATE VI

Pollen of *Viburnum* sects. VIBURNUM (A–D) and MEGALOTINUS (E, F): A, B, *V. macrocephalum* (Wilson 1835, A); C, D, *V. utile* (H. C. Chow 145, A); E, F, *V. punctatum* (Schneider 691, A); all type Ib. Scale bars = 10 μ m (A, C, E) or 1 μ m (B, D, F).

PLATE VII

Pollen of *Viburnum* sects. LENTAGO (A–C) and VIBURNUM (D–F): A, B, *V. prunifolium* (Bartholomew 1518, GH); C, *V. prunifolium* (Bush 7939, GH); D, *V. burejaeticum* (Ishidoya s.n., 1918, A); E, *V. veitchii* (Lingnan Univ. Herb. 78294, A); F, *V. mongolicum* (Rock 12480, A); all type Ic. Scale bars = 10 μ m (A, D, E) or 1 μ m (B, C, F).

PLATE VIII

Pollen of *Sambucus* (A, B), *Adoxa* (C, D), and Caprifolioideae tribes Caprifolieae (E) and Linnaeae (F): A, B, *Sambucus pubens* (Forbes 3433, GH); C, D, *Adoxa moschatellina* (Furuse s.n., 15 May 1961, A); E, *Lonicera chrysantha* (Purdum 6b, A); F, *Heptacodium jasminoides* (Keng 1068, A). A–D, type Ia; E, F, type IId. Scale bars = 10 μ m (A, C, E, F) or 1 μ m (B, D).

PLATE IX

Pollen of Caprifolioidae tribes Caprifolieae (A, B) and Diervilleae (C–F): A, *Leycesteria formosa* (Schneider 1394, A); B, *L. gracilis* (Forrest 9377, A); C, D, *Diervilla lonicera* (Jamison(?) s.n., 1930, GH); E, F, *Weigela florida* (Moran 4257, GH). A, B, type II_d; C–F, type II_f. Scale bars = 10 μm (A, C, E) or 1 μm (B, D, F).

PLATE X

Pollen of Caprifolioidae tribes Triosteae (A, B) and Linnaeae (C–F): A, *Triosteum aurantiacum* (Pennell s.n., 1924, GH); B, *T. perfoliatum* (McGregor 14287, GH); C, *Symphoricarpos albus* (Pease & Bean 26146, GH); D, *Kolkwitzia amabilis* (Rehder, Arnold Arb. 6475, GH); E, F, *Linnaea borealis* (Woodworth 388, GH). A–C, type II_e; D–F, type II_d. Scale bars = 10 μm (A, C, E) or 1 μm (B, D, F).

PLATE XI

Pollen of Caprifolioidae tribe Linnaeae (A–D) and Valerianaceae (E, F): A–C, *Abelia spathulata* (Furuse s.n., 7 May 1957, A); D, *Dipelta yunnanensis* (Rock 16150, A); E, F, *Nardostachys jatamansii* (Rock 14168, GH); all type II_d. Scale bars = 10 μm (A, C, E) or 1 μm (B, D, F).

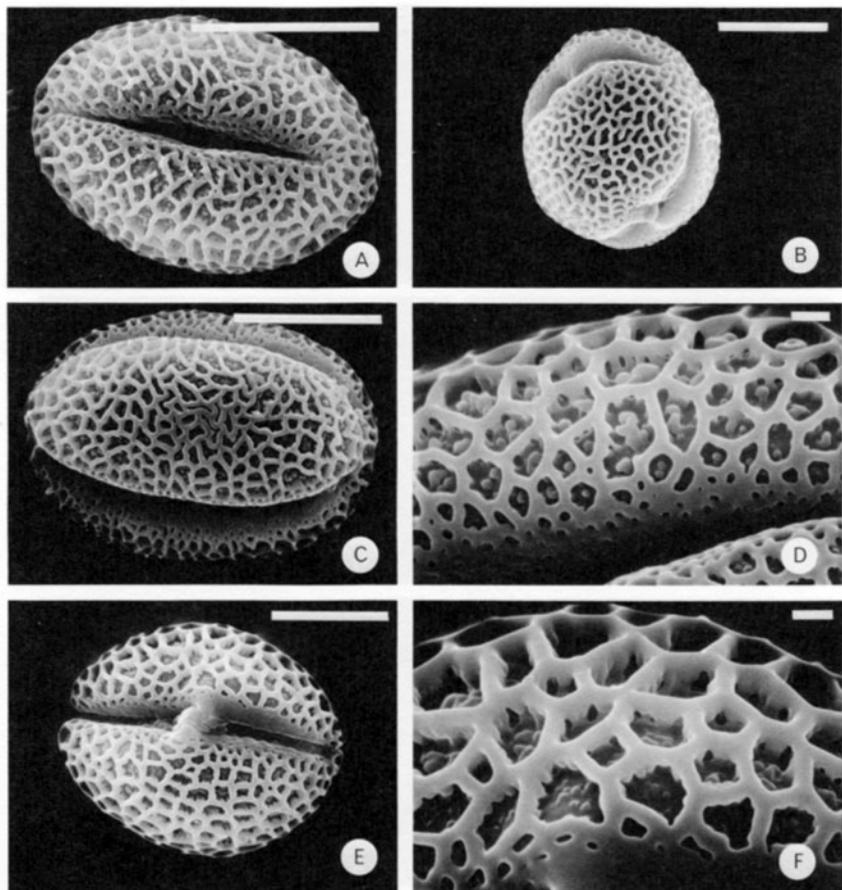


PLATE I

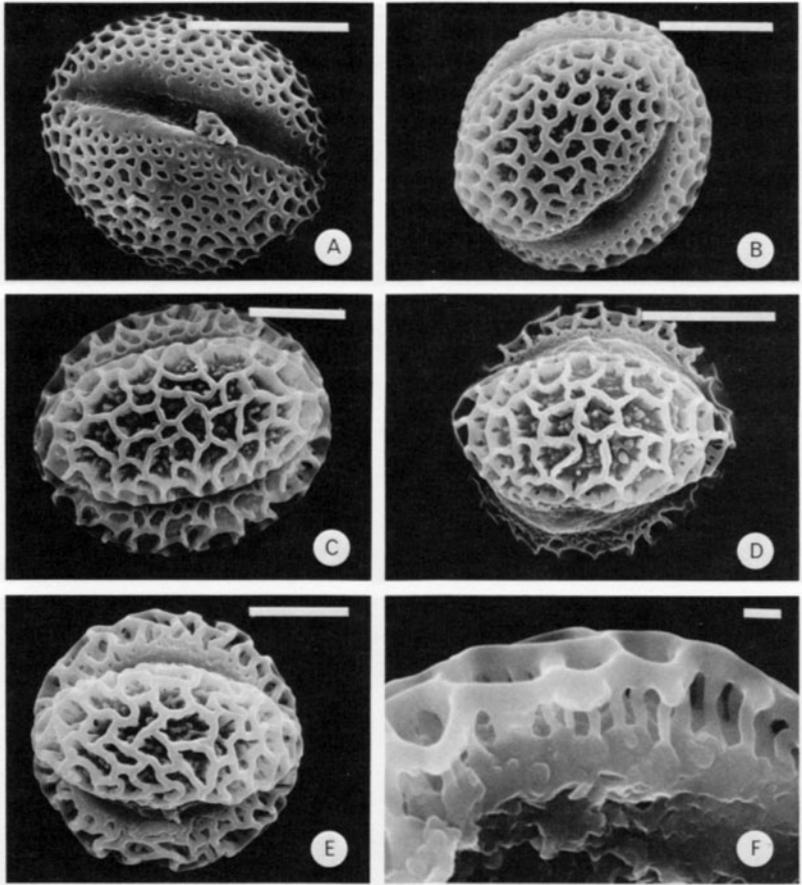


PLATE II

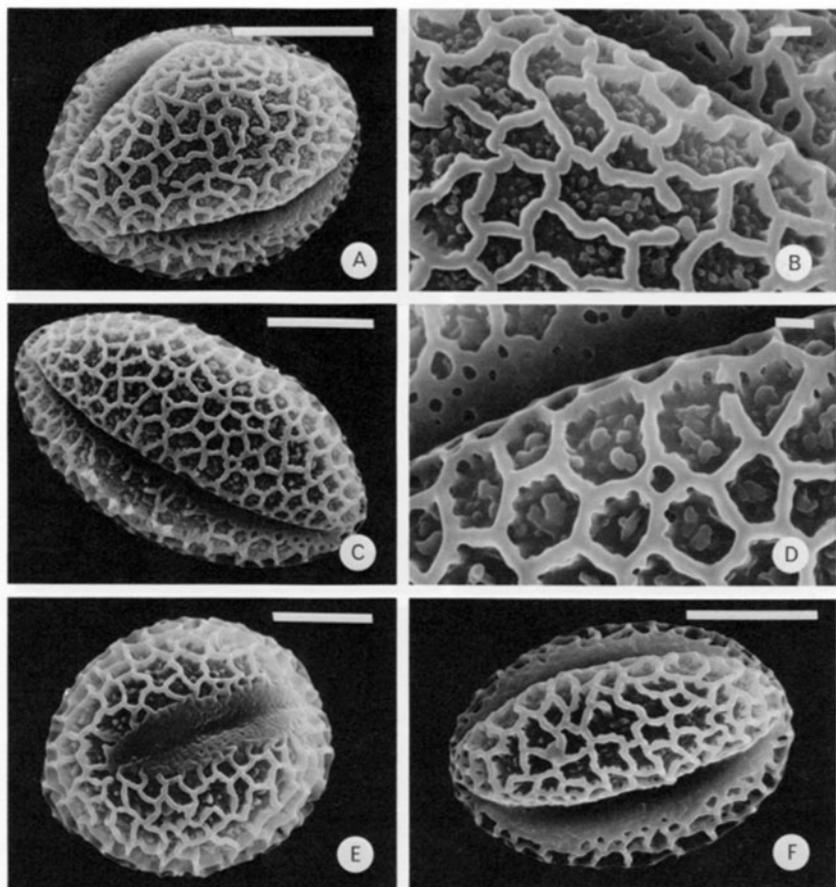


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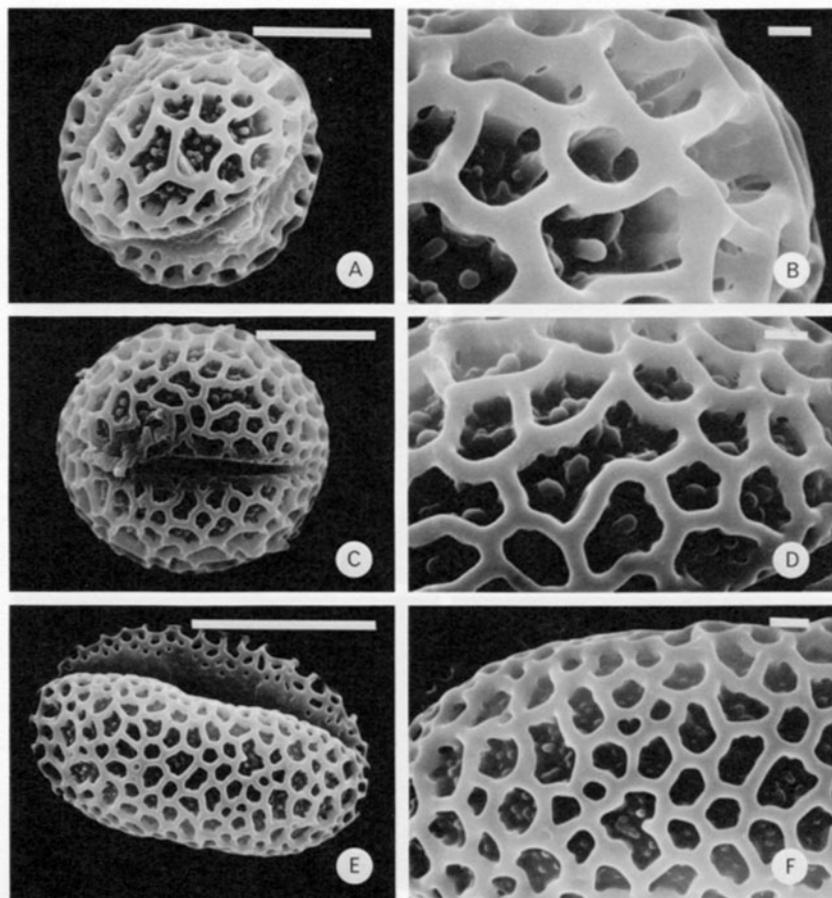


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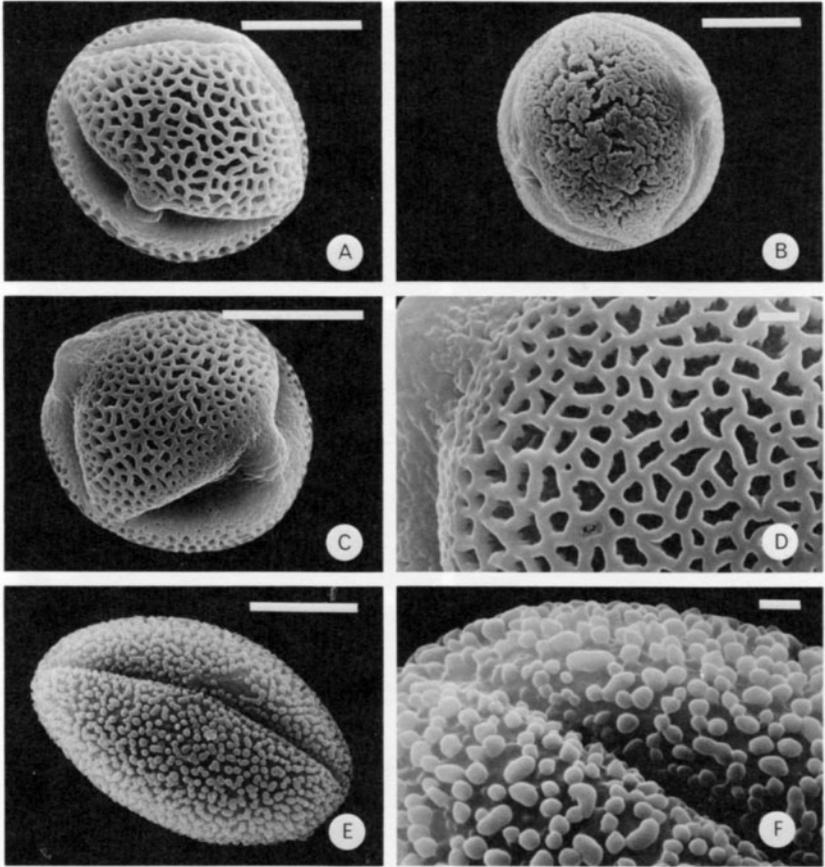


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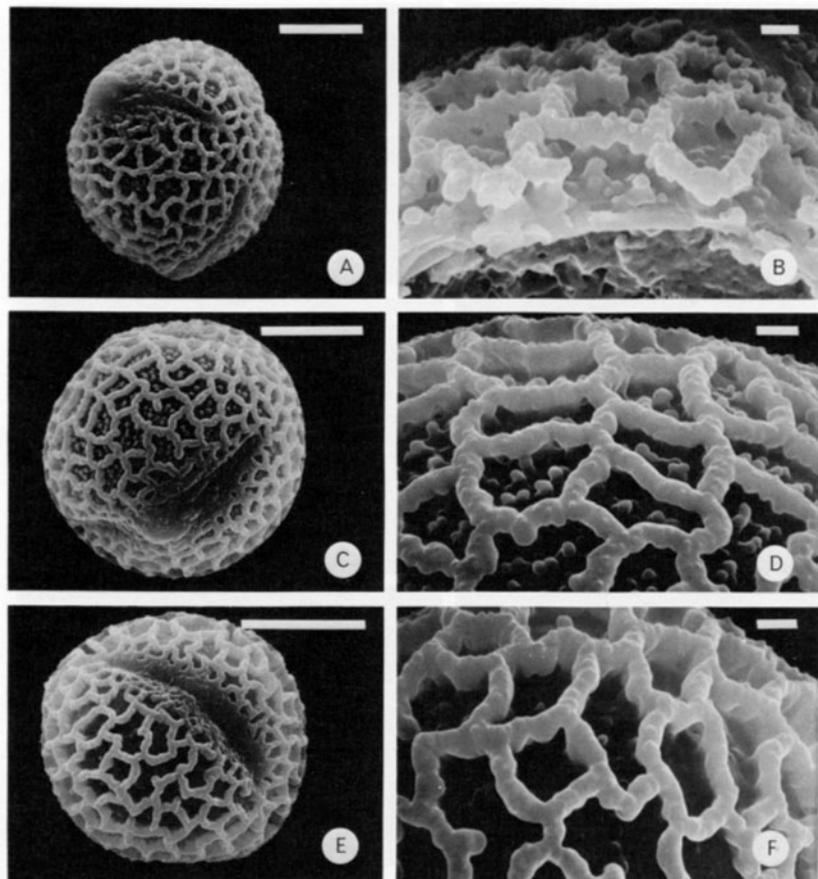


PLATE VI

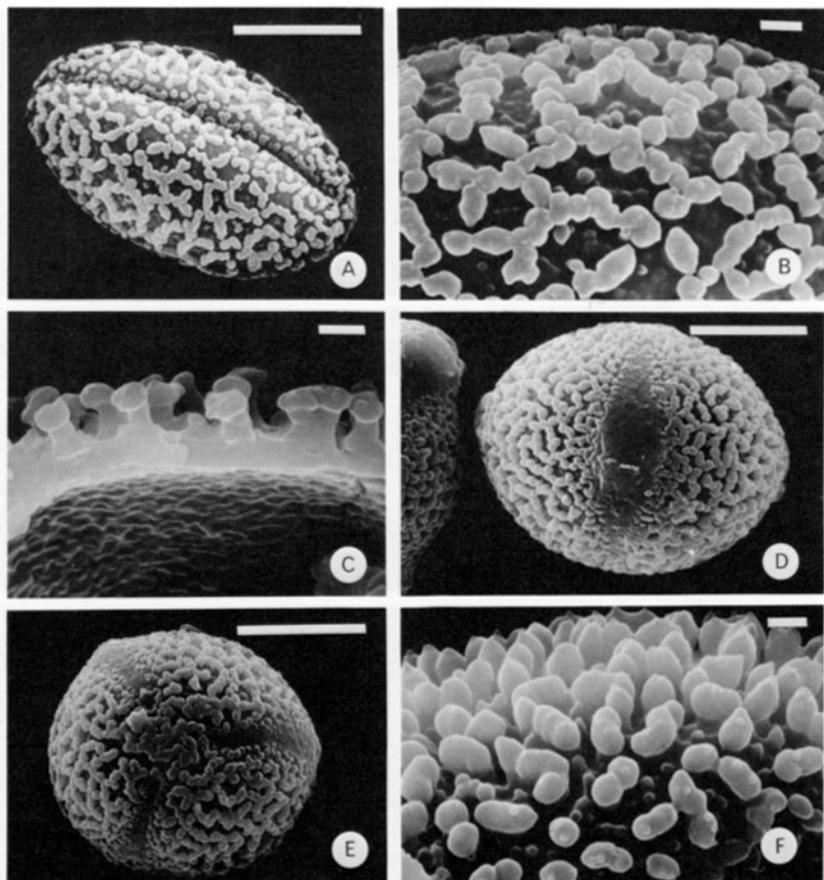


PLATE VII

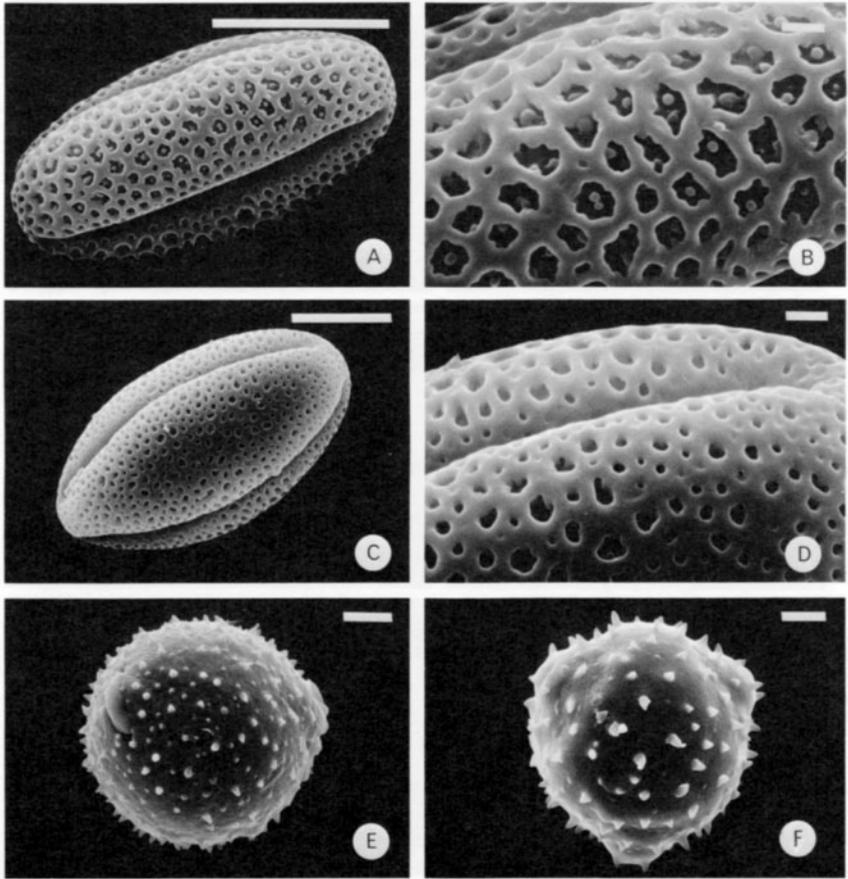


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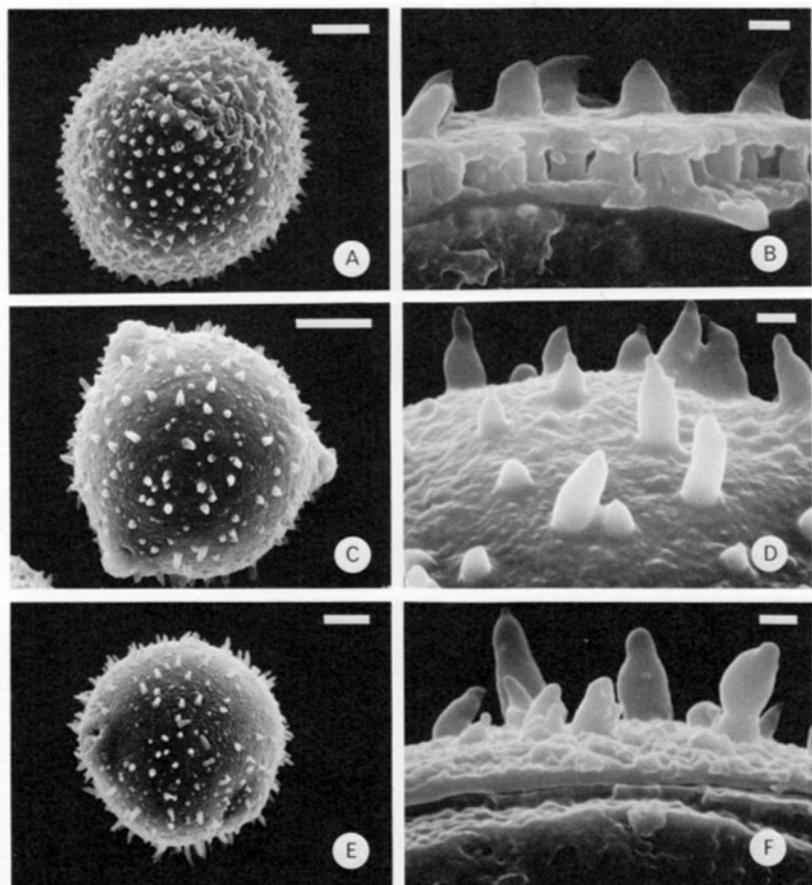


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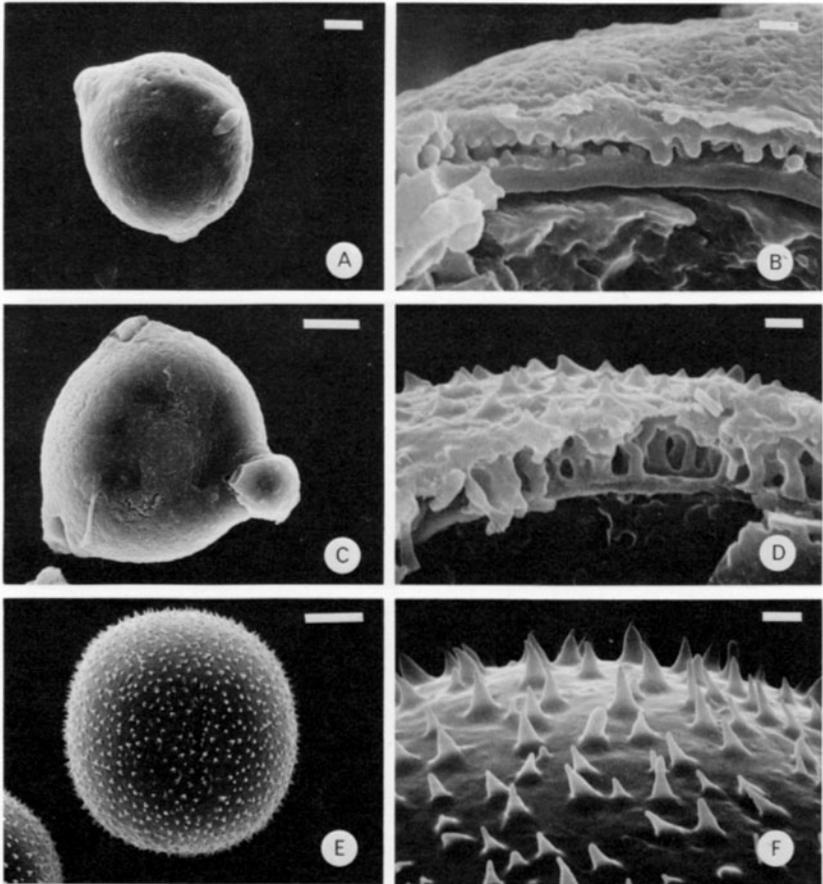


PLATE X

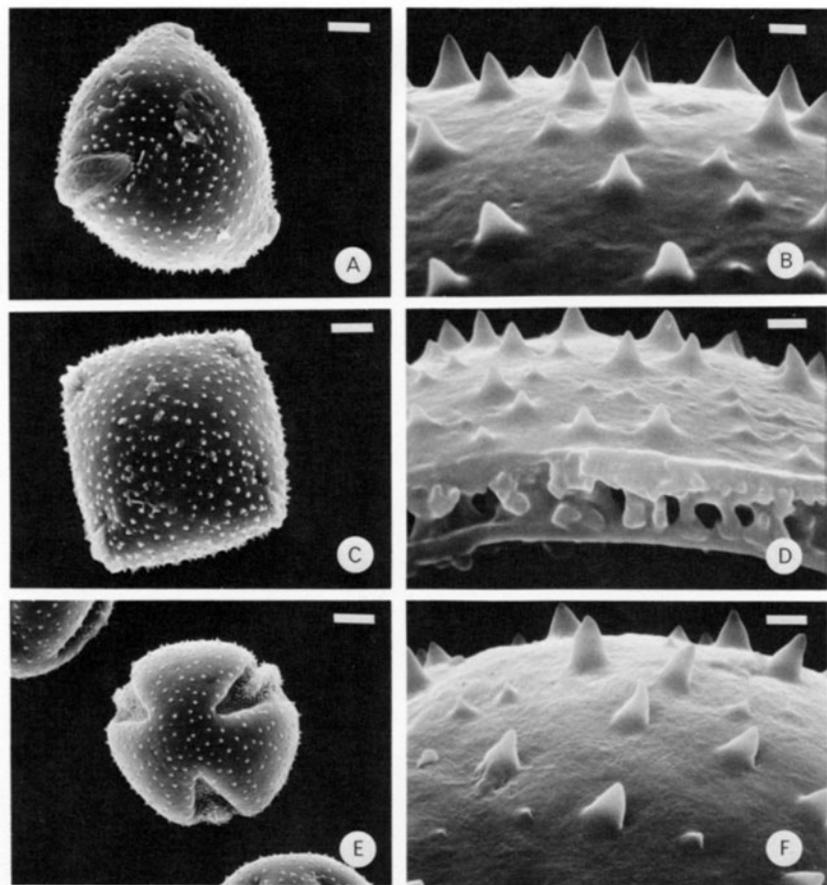


PLATE XI