THE GENUS CHAENOMELES (ROSACEAE)

CLAUDE WEBER

THE JAPANESE OR FLOWERING QUINCE, botanically, the genus *Chaenomeles* of the family Rosaceae, has been under cultivation in temperate areas of the world for over 400 years. Selections have been made and named in nearly every country where the plants are grown. Through the years, horticulturists have selected and propagated over 500 named varieties (cultivars). The classification of these many cultivars has been difficult, for unresolved problems exist in the morphology and taxonomy of the plants at the generic, specific, and varietal levels. Individual species exhibit a plasticity of form which is troublesome to botanists but of value in commercial horticulture. Hybrids are known involving two or all three species of the genus in both simple and in multiple crosses.

One of the goals of this study was to determine whether such a large group of cultivars of woody plants, largely of unknown parentage, could be placed in a systematic arrangement. The late L. H. Bailey, in his *Manual of Cultivated Plants*, did not attempt to include the cultivated varieties of *Chaenomeles*. He stated "To describe the main varieties of cultivated plants, even those customarily meriting Latin names, requires long and painstaking study, collections for the most part not in existence, historical perspective, a special application of nomenclature, and an appreciation of systematic values yet little developed." I have tried in the present study to meet these qualifications.

The Arnold Arboretum has an excellent representation of the common cultivars of *Chaenomeles* in its living collections. Through the cooperation of many other botanical gardens and commercial nurseries, representatives of most available cultivars were assembled for comparative studies. Directors and curators of herbaria and arboreta in many parts of the world have graciously loaned or given herbarium specimens of *Chaenomeles* species, varieties, and cultivars, and these have been an important aid in the historical and descriptive studies of the genus. The taxonomic, floristic, and horticultural literature in many libraries has supplied an "historical perspective." Of particular value in assembling the hundreds of "fancy names" applied to the selections of Japanese Quinces has been

the collection of nursery catalogues of the Massachusetts Horticultural Society. The "special application of nomenclature" and the "appreciation of systematic values" which Bailey pointed out were "little developed" in 1948, have both matured with the acceptance of the category of "cultivar" in the 1953 and subsequent editions of the *International Code of Nomenclature for Cultivated Plants.*

The genus *Chaenomeles* comprises only three species of moderate-sized shrubs adaptable to cultivation in temperate areas. By observing the plants through several years the seasonal changes in morphology could be observed; growing them in close proximity or in isolation, the natural and man-induced breeding habits could be studied. Collections of fruits, seeds, cuttings, and scions allowed experimentation on methods of germination, propagation, and subsequent development.

Living plants were the subject of this study when current observations could be compared with the descriptions published in a scattered supporting literature, and with an assemblage of herbarium specimens. Regrettably, a study of the basic species in China and Japan has not been possible and the known ecology of *Chaenomeles* is that of the plants in cultivation.

The taxonomic study of the genus *Chaenomeles* would have been impossible without examining numerous specimens dispersed in the herbaria of North America, Europe, and Asia. I wish to thank the directors and curators of the following institutions for the loan of herbarium specimens. They are cited according to the standard abbreviations of *Index Herbariorum.*

A   Arnold Arboretum of Harvard University, Cambridge, Massachusetts
AAH   Herbarium of cultivated plants, Arnold Arboretum, Jamaica Plain, Massachusetts
BM   British Museum (Nat. Hist.), London, England
G   Conservatoire et Jardin Botaniques, Genève, Switzerland
GH   Gray Herbarium of Harvard University, Cambridge, Massachusetts
K   Herbarium, Royal Botanic Gardens, Kew, Surrey, England
L   Rijksherbarium, Leiden, Netherlands
LE   Botanical Institute of the Academy of Sciences, U.S.S.R., Leningrad, U.S.S.R.
NY   New York Botanical Garden, New York
P   Muséum National d'Histoire Naturelle, Paris, France
US   U. S. National Museum, Smithsonian Institution, Washington, D. C.
TI   Botanical Institute, University of Tokyo, Hongo, Tokyo, Japan
UPSV   Växtbiologiska Institutionen, Uppsala Universitet, Uppsala, Sweden

Among the historical herbarium specimens, the "cultivars" were little represented. To fill this gap, numerous persons sent fresh material or took the time to press flowering branches, and to compile data. To the staffs of the following arboreta and nurseries, goes my appreciation for the gifts of living plants and herbarium specimens which added to both the living collection and the herbarium of cultivated plants of the Arnold Arboretum in Jamaica Plain, Massachusetts:

Beal-Garfield Botanic Garden, East Lansing, Michigan
Belmonte Arboretum, Wageningen, Netherlands
Dawes Arboretum, Newark, Ohio
Department of Parks, Rochester, New York
Du Pont Arboretum, Winterthur, Delaware
George Landis Arboretum, Esperance, New York
Holden Arboretum, Mentor, Ohio
Ida Cason Callaway Gardens, Pine Mountain, Georgia
Longwood Gardens, Kennett Square, Pennsylvania
Morris Arboretum, Philadelphia, Pennsylvania
Morton Arboretum, Lisle, Illinois
Mount Airy Arboretum, Cincinnati, Ohio
New York State Agricultural Experiment Station, Geneva, New York
New York Botanical Garden, New York
Orland E. White Arboretum, Boyce, Virginia
Planting Fields Arboretum, Oyster Bay, New York
Proefstation, Boskoop, Netherlands
Royal Botanic Gardens, Kew, Surrey, England
Stanley M. Rowe Arboretum, Cincinnati, Ohio
Station of Medicinal Plants, Kasukabe-Shi, Japan
Tudor House, Ripley, England
United States National Arboretum, Washington, D. C.
United States Dept. of Agriculture, Plant Introduction Station, Glenn Dale,
    Maryland
University of Connecticut, Storrs, Connecticut
University of Washington Arboretum, Seattle, Washington
Villa Taranto, Verbania-Pallanza, Italy
Bunyard Nursery, Maidstone, England
Darthuizer Nursery, Leersum, Netherlands
Fruitland Nursery, Augusta, Georgia
Harrison Nursery, New Zealand
Monrovia Nursery, Azusa, California
Phytotektor, Winchester, Tennessee
Wayside Gardens Nursery, Mentor, Ohio
Willis Nursery, Ottawa, Kansas

SYSTEMATIC POSITION OF CHAENOMELES IN THE MALOIDEAE

The genus *Chaenomeles* Lindley is assigned to the subfamily Maloideae [1] of the family Rosaceae. This natural division, under the name Pomaceae was suggested as a "fragmentum" by Linnaeus in 1763, who listed under it several genera such as *Pyrus* and *Crataegus*, but included also *Punica* and *Ribes* which are now placed in the Punicaceae and in the Saxifragaceae respectively. No description was given at that time. Since then, the justification for this taxon has not been contested by taxonomists. Some have treated the Maloideae as a separate family,[2] others as a tribe.[3] Currently it is widely accepted as a subfamily of the Rosaceae.[4]

The morphological characteristics of the Maloideae are: Trees or shrubs, unarmed or spiny. Leaves petiolate, alternate, simple or compound, with free stipules (at least on young shoots). Flowers regular, hermaphrodite (rarely unisexual by abortion), solitary, fasciculate or in terminal racemes, white, pink or red. Calyx campanulate-urceolate with 5 persistent or deciduous lobes. Petals 5, unguiculate, inserted in the throat of the calyx. Stamens 10–60, inserted at the same level as the petals, filaments free, anthers introrse with 2 locules. Disc laminate or fleshy, dry or nectariferous. Ovary formed of (1) 2–5 carpels, more or less adherent to the calyx on their abaxial side, completely fused with it at maturity. Ovules anatropous, usually 2 (1 by abortion) in each locule, to indefinite (*Chaenomeles, Cydonia*). Styles 1–5, terminal, free or connate at the base. Pollen tricolpate. Fruit fleshy, usually a pome (exceptionally a berry), formed of the hypanthium, the carpels becoming chartaceous or cartilaginous, and sometimes dehiscing on the adaxial suture, to bony and indehiscent. Seeds ascending (or horizontal when numerous), testa coriaceous, or less often mucilaginous, raphe and chalaza apical (or subapical), endosperm lacking, embryo orthotropous with short and conical radicle and imperceptible plumule.

According to Metcalfe and Chalk (1950), the Maloideae can not be separated by anatomical characters from the other subfamilies of the

[1] According to the *International Code of Botanical Nomenclature*, the name Pomoideae, in current use, is incorrect as it is not based on a genus. The subfamily name Pomoideae should be replaced by Maloideae, based on *Malus* Miller.

Maloideae Weber, stat. nov. Type: *Malus* Miller.

Malaceae Small, Fl. Southeast. U.S. 529. 1903.

[2] Pomaceae: Lindley, 1822, 1847; Bartling (Pomacées), 1830; Spach, 1834; Meisner, 1836–43; Endlicher, 1841; Walpers, 1843; Hoffmann, 1846; Roemer, 1847; Decaisne, 1874; Dippel, 1893; Burgerstein, 1896a & b, 1898a & b. Malaceae: Small, 1903, 1905; Bessey, 1915.

[3] Pomoideae: Jussieu, 1789. Pomaceae: De Candolle, 1825. Pomeae: Bentham & Hooker, 1865.

[4] Pomeae: Gray, 1842; Koehne, 1893. Pomoideae: Focke, 1894; Dalla Torre & Harms, 1900–07; Ascherson & Graebner, 1906–10; Rendle, 1925; Wettstein, 1935; Diels, 1936; Skottsberg, 1940; Rehder, 1949; Lawrence, 1951; Benson, 1957; Emberger, 1960.

Rosaceae. The genera of the Maloideae have few characteristics in common, as is true in the other subfamilies of the Rosaceae. Variation in the stem structure occurs even in individual species of *Chaenomeles* comparable to that recorded by Aubertot (1910) in the genera *Pyrus, Crataegus,* and *Prunus.* The Maloideae (except *Osteomeles*) have exclusively solitary vessels, while most of the other Rosaceae have a tendency to have a few together. They have fibers with fewer bordered pits on the tangential wall than on the radial walls, while the other Rosaceae, except some species of *Spiraea* have pits equally numerous on both walls. The only leaves with glandular teeth are found in *Chaenomeles, Pyrus, Sorbus,* and *Crataegus,* all members of the Maloideae.

If the Maloideae do not stand apart anatomically from the other subfamilies of the Rosaceae, the genera do so cytologically. According to Sax (1931, 1932, 1934) the basic chromosome number is 17 in all genera of the Maloideae, while it is 8 and 9 in the Spiraeoideae, 7 and 9 in the Rosoideae, 8 in the Prunoideae. This has been confirmed by all subsequent authors, Moffett (1931), Darlington (1945), Delay (1950–51), Cave (1958, 1959, 1960) and Löve and Löve (1961). Only *Quillaja brasiliensis* Mart., which undoubtedly belongs (by its morphology) to the subfamily Spiraeoideae, and has always been placed there by botanists, presents an exception by having 17 pairs (Bowden, 1945). Polyploidy occurs in the whole family Rosaceae, being limited to tri- and tetraploidy in the Maloideae. Darlington and Moffett (1930) suggested that the 17 pairs of chromosomes in *Pyrus* are made up from a basic number of 7 by duplication of 4 pairs and a triplication of 3 pairs of chromosomes. Sax (1932) rejected this idea and proposed that the Maloideae originated by hybridization of members of two different subfamilies, most likely belonging to the Spiraeoideae and to the Rosoideae. The Maloideae would thus be allotetraploid.

In geographic origin, the Maloideae are nearly restricted to the northern temperate hemisphere. Sax (1931) notes that 15 of the 18 genera enumerated by Rehder (1927) are represented by Asiatic species. He concluded that the Maloideae must have originated in Asia before starting their migration toward America (1 genus *Osteomeles* in Hawaii), Europe (1 genus *Chamaemeles* localized in Madeira), and North Africa. Only *Hesperomeles* reached South America, following the Andes as far as Chile.

There is no argument among taxonomists about the genera to be included or excluded from the Maloideae. Difficulty arises, however, when one has to determine the limits of the genera of the Maloideae, for many intergeneric hybrids are reported.

The genera recognized by Rehder (1949) are the following: *Amelanchier* Medicus, *Aronia* Medicus, *Chaenomeles* Lindl., *Cotoneaster* Ehrhart, *Crataegus* L., *Cydonia* Miller, *Docynia* Decaisne, *Eriobotrya* Lindl., *Malus* Miller, *Mespilus* L., *Osteomeles* Lindl., *Peraphyllum* Nuttall, *Photinia* Lindl., *Pyracantha* Roemer, *Pyrus* L., *Rhaphiolepis* Lindl., *Sorbus* L., *Stranvaesia* Lindl. To these should be added the genus *Chamaemeles* Lindl. and *Hesperomeles* Lindl. which are not cultivated, and the hybrid
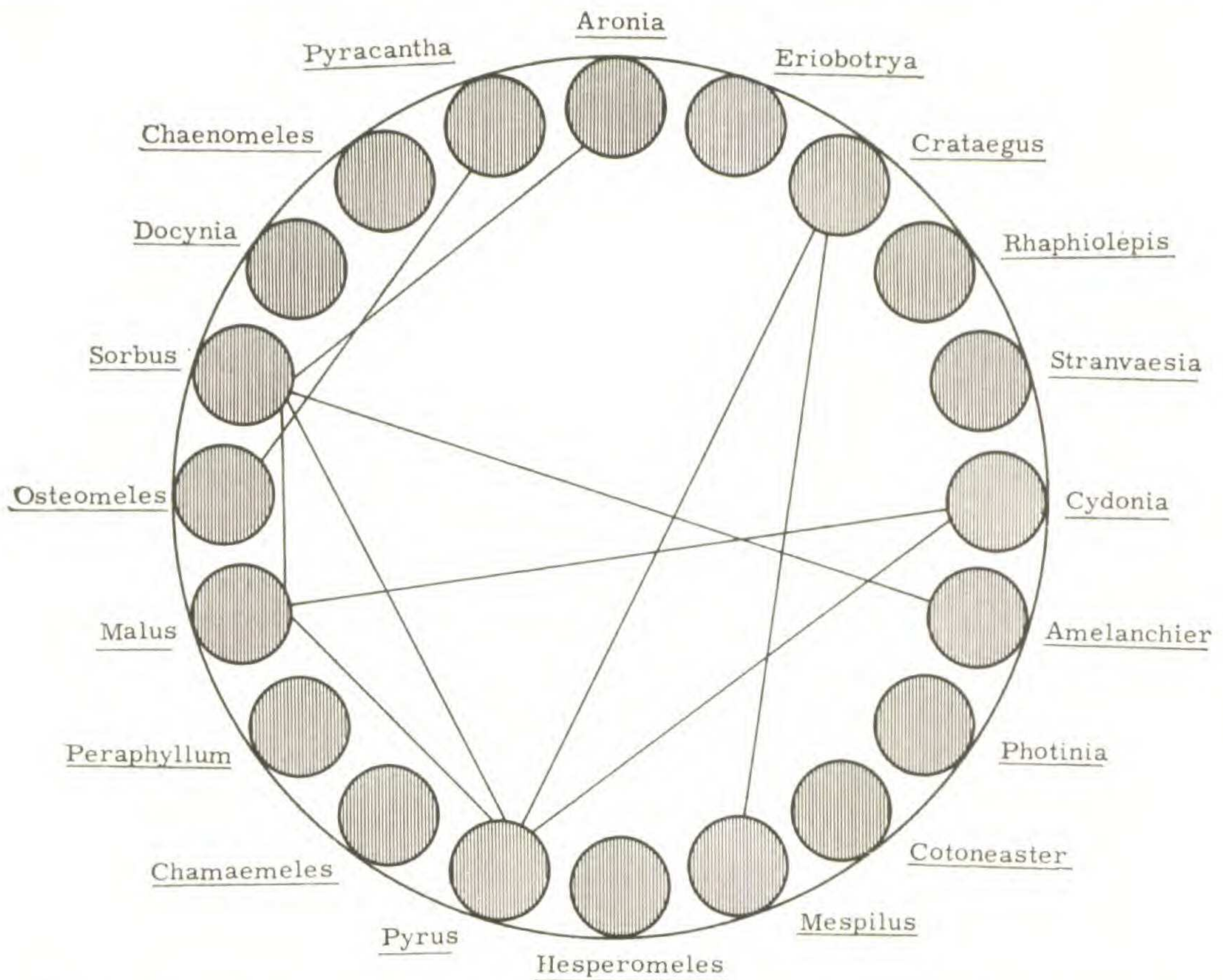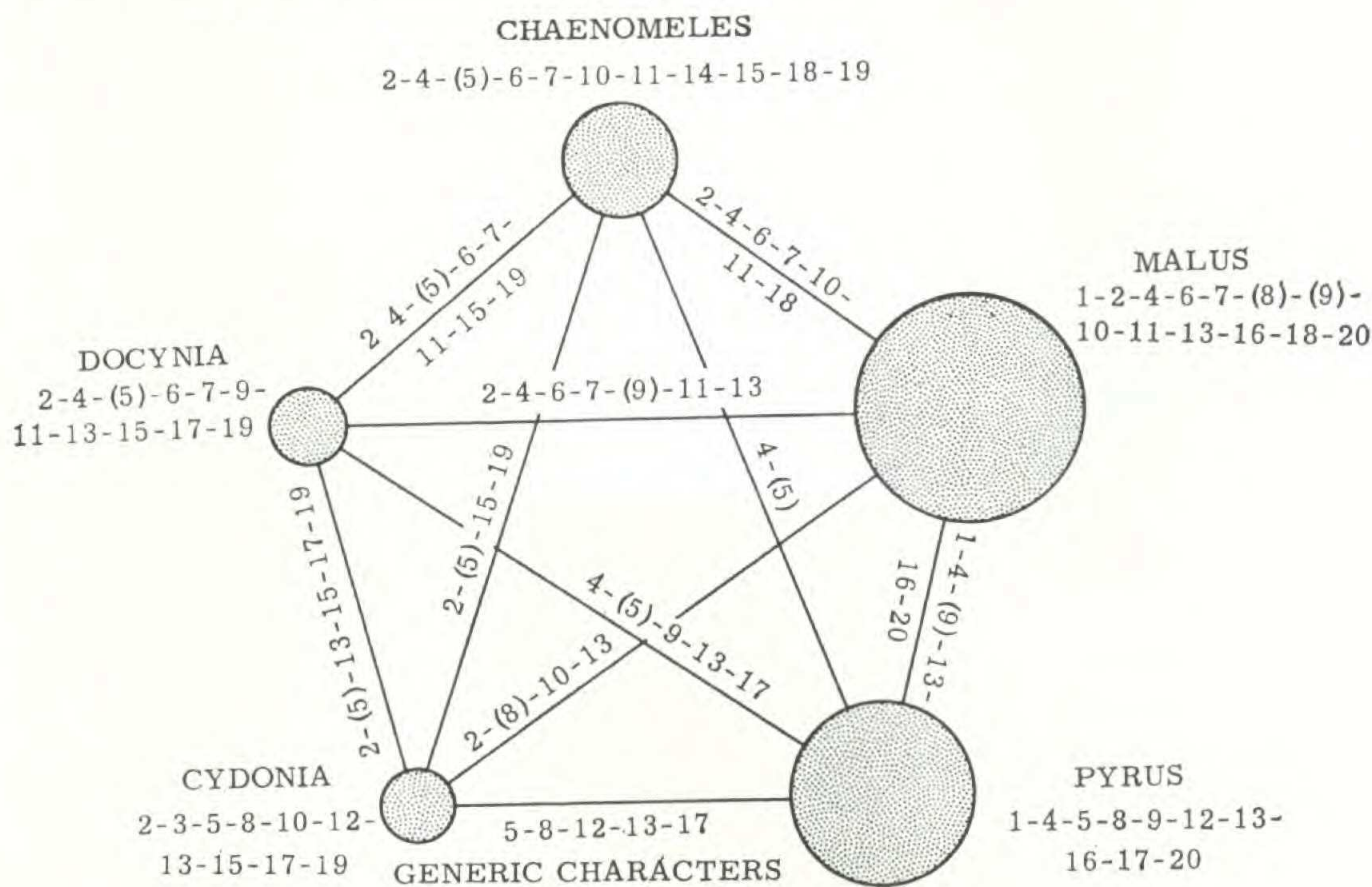
FIG. 1. Sexual intergeneric hybrids in the Maloideae. The genera are not arranged according to their affinities as such an arrangement would make the plate difficult to read.

genera *Amelasorbus* Rehder (*Amelanchier* × *Sorbus*), *Crataegomespilus* Simon-Louis (*Crataegus* × *Mespilus*), *Pyracomeles* (*Osteomeles* × *Pyracantha*), *Pyrocrataegus* Daniel (*Crataegus* × *Pyrus*), *Pyronia* Veitch (*Cydonia* × *Pyrus*), *Sorbaronia* Schneider (*Aronia* × *Sorbus*), *Sorbopyrus* Schneider (*Pyrus* × *Sorbus*). According to Rehder (1940), the cross *Cydonia oblonga* × *Malus* is reported to have been raised by I. V. Michurin, while Sax (in litt.) mentioned that the cross *Malus* × *Pyrus* was produced in Australia (FIG. 1).

Within the subfamily Maloideae, the genus *Chaenomeles* is most closely related to the genus *Cydonia*, with which it shares the character, unusual in the Maloideae, of an indefinite number of seeds in each locule. *Cydonia* and *Chaenomeles* have been placed in the same genus, namely *Cydonia* Miller, by numerous authors.[5] By others, *Chaenomeles* is considered a

[5] Persoon (1807), Loiseleur-Deslongchamps (1815, 1817), Sweet (1818, 1827), Hayne (1822), Guimpel, Otto & Hayne (1825), Siebold (1830), Loudon (1838), Endlicher (1840), Miritzi (1845–46), Van Houtte (1849), Planchon (1849), Lemaire (1856), Verschaffelt (1856) Courtin (1857), Hoffman & Schultes (1864), Wenzig (1874; *Chaenomeles*, 1883), Moore (1875), Nicholson (1884), Goldring (1888, 1891), Frahm (1898), Palibin (1898), Engler & Diels (1900), Ito (1900), Rehder (1900; *Chaenomeles*, 1914), Burgerstein (1901), Hemsley (1901a & b), Schumann (1901), Muth (1902), Bean (1903, 1914, 1930; *Chaenomeles*, 1951), Grignan (1903), Veitch (1903–04), Beckett (1907, 1909–10), Makino (1908), Nakai (1908, 1909; *Chaenome-*

section of *Cydonia*.[6] *Chaenomeles* is also related to *Pyrus*, and to *Malus* if this taxon is separated from *Pyrus*. *Chaenomeles japonica* (Thunb.) Lindl. ex Spach, the type species of the genus, was described first by Thunberg (1784) as a species of *Pyrus*. As late as 1902, some authors still joined *Chaenomeles* (and *Cydonia*) to *Pyrus*.[7] Andrews (1807) transferred *Pyrus japonica* Thunb. to *Malus*.

CHAENOMELES
2-4-(5)-6-7-10-11-14-15-18-19

MALUS
1-2-4-6-7-(8)-(9)-
10-11-13-16-18-20

DOCYNIA
2-4-(5)-6-7-9-
11-13-15-17-19

2-4-6-7-(9)-11-13

CYDONIA
2-3-5-8-10-12-
13-15-17-19   5-8-12-13-17   GENERIC CHARACTERS

PYRUS
1-4-5-8-9-12-13-
16-17-20

1. Vernation involute.
2. Vernation conduplicate.
3. Aestivation contorted.
4. Aestivation imbricate.
5. Flowers on leafy shoots.
6. Flowers on old wood.
7. Sepals erect at anthesis.
8. Sepals reflexed at anthesis.
9. Petals white.
10. Petals usually colored (pink to red).
11. Stamens in two rows (15-60).
12. Stamens in one row (20-30).
13. Styles free (sometimes coalescent).
14. Styles fused in a column.
15. Stigma decurrent.
16. Stigma discoid.
17. Grit-cells numerous and in the whole hypanthium.
18. Grit-cells absent (or in a row in the exocarp)
19. Numerous (3-24) ovules in each locule.
20. Two ovules only in each locule.

FIG. 2. Affinities between the genera closely related to *Chaenomeles*. The size of the circle is in proportion to the importance of the genus. The characters indicated between parentheses occur occasionally, or in a minority of the species. The characters given odd numbers are considered more primitive than those having even numbers.

les, 1916a), Mottet (1917), Cardot (1918), Richards (1923), Späth (1930), Diels (1936), Faulkner (1941), Hurley (1948), Jex-Blake (1950), Emberger (1960).

[6] De Candolle (1825), Don (1832a), Focke (1894).

[7] Thunberg (1784), Murray (1784), Vitman (1789), Willdenow (1800), Sims (1803), Jacquin (1809), Aiton (1811), Loddiges (1821, 1829), Sprengel (1825), Morris (1826), Morren (1851), Miguel (1867), Koch (1869), Franchet & Savatier (1873-75;

Another closely related genus, *Docynia*, shares with *Chaenomeles* the character of numerous stamens in two rows (40–60 in *Chaenomeles*, 30–50 in *Docynia*). The type species of the taxon, *Docynia indica* (Colebrooke) Decne., was described first as *Pyrus indica* by Colebrooke (in Wallich, 1831), then transferred to *Cydonia* by Spach (1834), before Decaisne (1874) established the genus *Docynia*.[8]

The genus *Pseudochaenomeles* Carrière (1882), based on an unreliable fruiting characteristic of *Chaenomeles japonica* (Thunb.) Lindl. ex Spach (as *C. maulei*) as opposed to *C. speciosa* (Sweet) Nakai (as *C. japonica*), was not maintained by its author. The genus *Pseudocydonia* Schneider, which was first established as a section of *Chaenomeles* by Schneider in May 1906, was raised by him to generic rank in November of the same year, to include *Cydonia sinensis* (Dum.-Cours.) Thouin, will not be considered here. These two genera are not at present recognized by any taxonomist.

In FIGURE 2 an attempt is made to show the affinities between the genera related to *Chaenomeles*. The characters chosen are arranged to offer an alternative. The one given the odd number is supposed to be more primitive than the character having an even number. If it were possible to show the entire subfamily Maloideae on a multidimensional system, it would help to understand the generic limits and the phylogeny of the group. This is not practical for the genera are too numerous and many are not known well enough at the present time.

Because of the wide divergence of opinion among taxonomists as to how many genera should be recognized in the Maloideae, it is presumptuous to attempt to discuss the evolution of the different genera without having studied the whole group carefully. From its geographic distribution, as shown above, from the morphological characters of the inferior ovary and the syncarpic fruit, and from a consideration of the high basic chromosome number, the subfamily Maloideae appears to be of more recent origin than the other subfamilies of the Rosaceae.

The Maloideae is closest morphologically to the Spiraeoideae and the Rosoideae, and closest anatomically to the Prunoideae. The genera of the Maloideae are closely related, as shown by their morphology, and supported by the graft compatibilities (FIG. 3) and numerous sexual hybrids. This was shown by Decaisne in 1872, and Sax in 1931, each of whom wrote that botanists having a tendency for lumping could go as far as to consider all the Maloideae one genus. Burgerstein (1896a) suggested on the basis of the anatomical structure: "Alle untersuchten Pomaceen — 130 Arten (inclusive Hybriden und Varietäten) — die sich auf 16 Gattungen

Franchet in *Chaenomeles*, 1883), Hemsley (1873; *Cydonia*, 1901), Kurz (1873), Masters (1874a), Neumann (1875), Smith (1875), Hooker (1884), Tanaka & Ono (1891), Arnott (1902).

[8] Abnormal flowers of *Chaenomeles speciosa* observed in the spring of 1961 had the styles fused in a hairy cone protruding above the insertion of the stamens and petals, very much like *Docynia*, and in the extreme cases, no ovules were present. Lobed leaves, frequent in *Chaenomeles* seedlings occur regularly in juvenile leaves of *Docynia indica*.
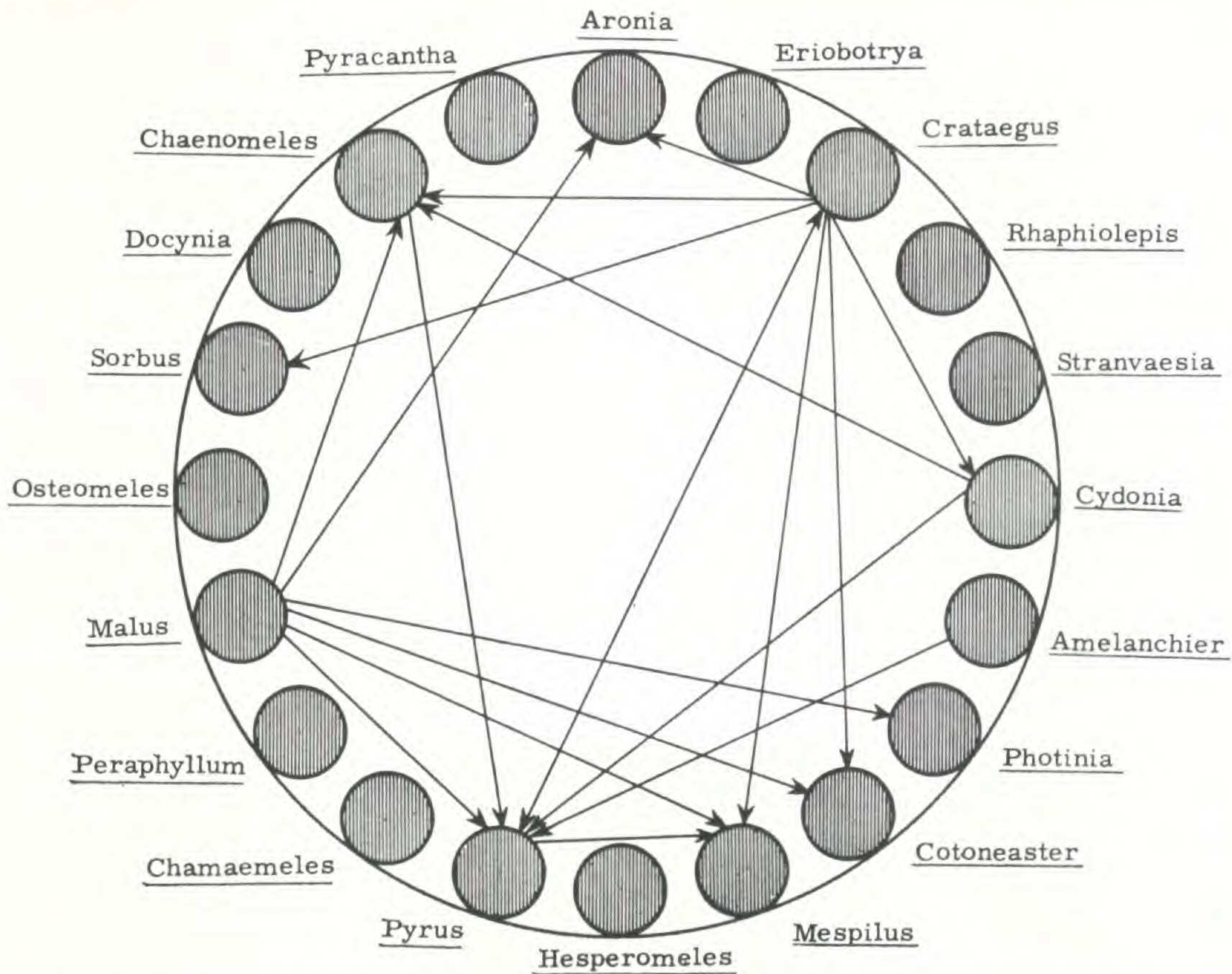
FIG. 3. Grafting affinities of the Maloideae. The arrows indicate the direction from understock to scion.

vertheilen, zeigten im Wesentlichen einem Uebereinstimmenden Holzbau." The genera of the Maloideae are thus delimited mostly for the sake of convenience, and there will always be disagreement among taxonomists as to how many genera and which ones should be recognized.

The position of the genus *Chaenomeles* within the Maloideae is not clear. The numerous seeds in each locule indicate that *Cydonia* and *Chaenomeles* are primitive in this respect, and *Pyrus* and *Malus*, with only two seeds in each locule, are more advanced. The characteristic of the number of seeds induced Decaisne (1847) and Wenzig (1874 to 1883), in accordance with most of the authors recognizing only the two genera *Cydonia* (including *Chaenomeles*) and *Pyrus* (including *Malus*), to consider *Chaenomeles* most closely related to the genus *Cydonia*. On the other hand the morphology of the flower (stamens and styles) and of the fruit, and the presence or absence of grit cells placed *Chaenomeles* closer to *Malus*, and *Cydonia* closer to *Pyrus*. Koehne (1890) suggested an evolutionary scheme of the Maloideae, in which the genera evolved from *Sorbus* in six distinct lines, and he is also followed by Dippel (1893).

Unfortunately, the results provided by anatomical investigations do not agree with the conclusions reached by observations on the gross morphology. The anatomical investigations are also contradictory, for so far only one characteristic has been considered at a time. If the size of the vessels and the number of cells in the width of the vascular rays are considered

alone (Burgerstein 1896a, 1896b, 1898a, 1898b), *Chaenomeles* is closer to *Pyrus*, and *Cydonia* to *Malus*. If the presence or absence of a tertiary thickening in the vessels (Burgerstein 1898a) or the anatomy of the leaf (Gérard, 1884) are the only characters chosen, *Chaenomeles* and *Cydonia* are more closely related, as are *Pyrus* and *Malus*. The divergence of conclusions reached by independent study of the gross morphology or of the anatomy has been pointed out by Burgerstein (1896a), and Folgner (1897).

The taxon *Cydonia sinensis* presents difficulties in the distinction of the four closely related genera *Chaenomeles*, *Cydonia*, *Pyrus* and *Malus* (*Docynia* not being well enough known). This species has been placed successively in the four genera mentioned, in *Malus* by Dumont de Courset (1811), in *Cydonia* by Thouin (1812), in *Pyrus* by Poiret (1816), and in *Chaenomeles* by Koehne (1890). Schneider (1906a) established a special section for *C. sinensis* which fitted so poorly in *Chaenomeles* that within the same year he (Schneider, 1906b) raised it in rank to form the monotypic genus *Pseudocydonia*. According to Burgerstein (1898b), *C. sinensis* is "eine Brücke" between *Cydonia oblonga* Miller and *Chaenomeles speciosa*.

The basis for the transfer of *Cydonia sinensis* to *Chaenomeles* by Koehne is not clear. He wrongly stated that the styles are fused. The only characteristics *Cydonia sinensis* shares with *Chaenomeles* are the glabrous fruits with deciduous sepals, serrate leaves, and an Asiatic origin (extinct in the wild), while it shares more than 35 other generic characters with *Cydonia*. Moreover, all the three species of *Chaenomeles* have fertile hybrids between them, while crosses of *Chaenomeles* species with *Cydonia sinensis* have been attempted several times but have always failed. The fact that *Cydonia oblonga* has entire leaves while *C. sinensis* and *Chaenomeles* have serrate leaves must not be given much weight, even if convenient in a key. The first few leaves of *Cydonia oblonga* seedlings are often serrate and later appear with entire margins. The fact that the calyx of *Cydonia sinensis* is deciduous, in contrast to the persistent calyces of *Cydonia oblonga*, is also unimportant for this character varies on individual shrubs of *Chaenomeles*. Rubsow (1944) noted that all the primitive species of *Pyrus* have a deciduous calyx, while the more advanced species have a persistent calyx.

Burgerstein (1896a, 1896b, 1898b) studied the wood structure of *Cydonia sinensis* and found it to correspond more closely with the structure of *Chaenomeles* wood than with that of *Cydonia* wood. From his wood study, this author considered *Cydonia* and *Chaenomeles* as distinct, and the latter as including *C. sinensis* (as suggested by Koehne). In 1898 he observed for the first time the flowers of *Cydonia sinensis* on a tree growing in the Vienna Botanic Garden. Burgerstein was forced to admit that the styles are free and not fused, as he had previously believed. This fact must have disturbed him, for in 1901 he published a paper, accompanied by a good colored plate, entirely devoted to this species, which he reassigned to *Cydonia*. His anatomical key to the genera of the Maloideae

did not correspond to the morphological affinities he observed in the styles, and he united *Cydonia* and *Chaenomeles* again. Burgerstein is the only botanist so far who arrived at this conclusion after having studied both genera.

Excluding Burgerstein's opinion of the validity of the genus *Chaenomeles*, all other taxonomists who have studied *Cydonia* and *Chaenomeles*, namely Bean (after 1951), Carrière, Decaisne, Koehne, Koidzumi, Nakai (after 1916), Rehder (after 1914), and Wenzig (after 1883) have concluded that they are distinct genera. This conclusion might have been reached more easily if the limits of the two genera were not somewhat blurred by the incorrect position in which Koehne placed *Cydonia sinensis*. There is a tendency often to delay a change of name in a nursery catalogue, sometimes even against horticultural knowledge. It is shown here in the reluctance of Goldring, Grignan, Hemsley, Mottet, Planchon, Späth, and Sweet to accept the conclusion that *Chaenomeles* and *Cydonia* are distinct; and some even persisted in placing *Chaenomeles* species in the genus *Pyrus*.

In spite of the reservations of some botanists and horticulturists, the recognition of the genus *Chaenomeles* is justified. The three species it includes, *C. japonica*, *C. speciosa*, and *C. cathayensis* form a good taxonomic unit, based on their geographic distribution, their morphology, and their breeding behavior. The three species do cross with each other but do not cross with species of other genera. Within the Maloideae, *Chaenomeles* possesses characteristics more primitive than the other genera, such as numerous seeds and numerous stamens in 2 rows, but it also shows a tendency toward unisexual flowers, which is to be considered an advanced character.

The genus *Chaenomeles* has not been found as a fossil in Japan (Tanai, 1961), in spite of the fact that several Rosaceae were recorded in the Tertiary flora of the island and that the leaves of Japanese Quinces should be easily recognized by their serrations. *Chaenomeles* is perhaps a relatively recent immigrant in Japan, having evolved in China in the Yunnan region, where two of its species are still found.

MORPHOLOGY AND ANATOMY

The morphology of the genus *Chaenomeles* was studied on living specimens observed over a period of three years. These observations showed the unsuspected extent of variability existing in each individual and permitted consideration of the characters commonly used to distinguish the genus *Chaenomeles* from closely related genera, as well as those used to separate its species. A survey was also made of the anatomical characters of *Chaenomeles* to determine if any feature would distinguish this genus among the Maloideae.

Roots. The roots are numerous, fasciculate, and relatively superficial. In an old shrub, there may be several main roots, reaching up to 3 cm. in diameter.

André (1872) reports having observed in the Simon-Louis Nursery, Metz, France, roots which when dug up to make root cuttings, were bearing flower buds. One of these root fragments, left on a table, produced flowers which opened within a few days. André's figure shows flowers with long peduncles, but on an otherwise normal spring inflorescence. Twice, at the Arnold Arboretum, we observed flowers coming up through the ground, without being able to ascertain whether they were attached to a root or to a rhizome. The inflorescences were of a special type, and will be discussed further on.

Habit. There are three growth-forms in *Chaenomeles* corresponding to the three species. *C. japonica* has numerous spreading branches which completely cover the ground, and when in contact with it have a tendency to form adventitious roots. *C. speciosa* possesses many branches which are erect at first, and then spreading. Plants of this species increase by new suckers which, when left without control, may cover extensive areas. *C. cathayensis*, in contrast, possesses only a few straight, erect branches, with numerous short lateral branchlets terminated by a spur. These plants have a stiff appearance and can be trained as small trees.

The interspecific hybrids usually show an intermediate shape, but there are a few exceptions. *C. × superba* 'Crimson and Gold' tends to spread, forming a mat up to 50 cm. high on the ground, as would a pure *C. japonica*. Two cultivars of *C. speciosa*, 'Spitfire' and 'Starlight' have a characteristic vase shape due to numerous straight branches. Several cultivars show abnormal branching as indicated by their names 'Fastigiata', 'Pendula', 'Contorta', and 'Tortuosa'. In 'Contorta' the mutation affecting the shape of the branches (which change direction at each node) is carried into the progeny, or at least part of it, even though the other parent has normal branching.

The method of training Japanese Quinces along a wall, in common use in England, indicates how the shape of a shrubby plant may easily be changed, even with a minimum amount of pruning. The natural shape seems also to be modified through the influence of heavy snow cover. The hybrids of *C. cathayensis* often lose their branches completely, due to cold. The parts protected by the snow usually survive and start new shoots the following spring. On old plants, the snow may produce an artificial spreading form by repeated elimination of the straight, erect branches. In very cold winters, flower buds of *Chaenomeles* freeze above the snow line. The hardiness of *C. japonica* is probably due to its low habit rather than to intrinsic physiological qualities.

Buds. There are three kinds of buds, leaf buds and flower buds, both well formed, and adventitious buds.

The pointed and round *leaf buds*, usually 1 to 2 mm. long, are covered by a few pubescent, loosely imbricate scales. There are no true terminal buds since the long shoots are either terminated by a spine, or keep growing until the fall, when they are killed back by frost. The vernation is con-

duplicate, in contrast to the involute vernation of *Pyrus* and of some species of *Malus*. When the leaf buds are dissected, numerous brown imbricate scales, ciliate at base, or with tufts of trichomes at base and apex, and varying in size, may be seen. Within are about 4 to 8 embryonic leaves, with petioles already visible by the end of the summer and, in the center, meristem which will produce the next year's long shoot. The glabrous, embryonic leaves appear entire, but are bordered by narrow, ovate, transparent glands, lined side by side, and directed toward the tip. When the leaves unfold, the petioles grow faster than the blades, representing at one time $\frac{1}{3}$ to $\frac{1}{2}$ of the leaf, but in mature leaves only $\frac{1}{5}$ to $\frac{1}{8}$ of the length. Before the inner leaves have finished unfolding, the glands may be seen to secrete liquid.

The *flower buds* are formed early in the fall. The 1 to 6 flowers contained in each bud start to expand at the end of the summer, breaking up the bud. Ciliate scales surround the young flowers which spend the winter in a very advanced stage. By October, the flower color can often be recognized. In fact, the flowers are ready to open in a few days, at about any time from November, and often do, if the cold weather does not interrupt their development. This is why branches of Japanese Quinces are so easily forced for sale as cut flowers. In spite of this precocity of pigmentation of chlorophyll and anthocyanins, meiosis for most buds occurs in the spring.

The buds do not show specific differences in *Chaenomeles*. In order to identify the shrubs in winter condition, the shape of the branches, the spines, and the warting of the twigs normally present good characters for distinguishing the species. In cultivation, the abundance of interspecific hybrids showing intermediate characters renders this method very uncertain, however.

Shoots and spines. There are two main types of shoots in *Chaenomeles*, as in the closely related genera, which represent long and short shoots. These appear at different times of the year and spend the winter in distinctive stages, the long shoots as shoot "primordia," and the short shoots as "stemless" embryonic leaves.

The *short shoots* develop first, nearly simultaneously with the flowers, usually the first week of May in the climate of Boston. They appear on old branches as well as on the long shoots of the preceding year, without any indication of future development into long shoots. They bear four to eight fasciculate leaves varying widely in size, the outer ones being $\frac{1}{10}$ to $\frac{1}{2}$ the size of the inner ones. The outer leaves are frequently malformed, subentire (but with glands), and often emarginate or with a dry tip. They are usually promptly caducous. As the inner leaves unfold, the glands terminating the veins form the tip of each serration, alternating with a gland in each indentation.

On the long shoot of the preceding year, a spine axillary to the leaves with a bud on each side may often be observed. In *C. cathayensis*, one of these buds develops into a short shoot which may be located on the right,

or on the left of the spine, but it will be on the same side all along the branch. The buds on the other side of the spines will remain dormant under a large scale, for one or a few years, and may later produce flowers. In *C. japonica*, buds produced basally on both sides of the spines usually produce short shoots, giving a characteristic bushy appearance to this species. *C. speciosa* normally does not have spines axillary to each leaf of a long shoot, but rather has one bud produced at each node. The leaves of the short shoots are produced within a few days. The shoots terminate in a bud, which may or may not produce a spine.

After the leaves have expanded on short shoots, and by the middle of May in New England, a second flush of growth takes place. From this time on, *long shoots* only will be produced until the following spring. Leaves of long shoots do not differ in shape or size, but they are accompanied by large, paired reniform stipules, contrasting with the exstipulate leaves of the short shoots. New long shoots appear at the apex of last year's long shoots, if these have been interrupted and partially killed back by frost. The last living axillary bud, or many of the upper ones, may at once start to produce long shoots. New long shoots rarely appear if the long shoot of the preceding year was terminated by a spine. Long shoots located at the tip of branches do not usually ramify during the first season. The straight lateral branchlets occurring at right angles with the main branches, typical of *C. cathayensis* and its hybrid *C. × californica*, are formed on long shoots during the second season. Each axillary bud will produce a long shoot which is terminated by a strong spine or spur. Very often flowers will be borne on these short branchlets and in *C. × californica* long shoots will appear as a continuous mass of flowers along most of their length.

Long shoots, when expanding, are usually covered with a short and scabrous tomentum. The trichomes are unicellular, unbranched, and slightly bulbous at the base. They fall off the first summer without leaving a scar in *C. cathayensis* and in *C. speciosa*. In *C. japonica* where the trichomes are more abundant, the bulbous hair bases persist and appear as dark warts on the shoots during the second year. As the twigs enlarge in girth, the warted epidermis is shed during the second summer, and is replaced by a smooth bark. The presence of warts on the second year twigs is a characteristic of *C. japonica* and its hybrids. The old warted epidermis persists longer around the nodes, and can sometimes be found after the second year. Temporary warts occur exceptionally in *C. speciosa*, and have been observed in at least one herbarium specimen from China, where hybridization with *C. japonica* is very unlikely.

Spines may be formed very early, axillary to a leaf in a long shoot, especially in *C. cathayensis*. Most of the time, however, they appear only in the summer, terminating either a short shoot, or a long shoot. They are slender at first, straight, and probably increase in diameter during the second year. Young spines show by their occasional pubescence, or the presence of buds, that they are modified long shoots. The spines are stouter and more abundant in *C. cathayensis*, more slender in *C. japonica*,

and show an intermediate condition in *C. speciosa* and in the interspecific hybrids.

A few cultivars have been named for a lack of spines, however, there are usually a few on old shrubs of these spineless cultivars. *C. speciosa* 'Contorta', and *C.* × *superba* 'Tortuosa', in addition to unusual branch form, possess hooked spines, the points of which are directed toward the base of the branch. The curvature is evident as early as the spines appear from the buds.

Abnormal production of long shoots has been observed in the following cases: after the shrubs have been killed back to the ground or severely damaged by frost; after application of a weed-deterrent; and after an extremely severe attack of insects.

After a killing frost, long shoots are produced by adventitious buds at the base of the plant. These shoots are abnormally vigorous. They grow and ramify very rapidly, reaching as much as 1 meter in length within a few weeks. The pubescence is reduced or completely absent, the epidermis shedding off soon after being produced. Spines often appear immediately, axillary to each leaf, at least in *C. cathayensis*. The leaves and stipules of these shoots attain greater size than those in the crown of the shrubs.

Following the application of a weed-deterrent (Simozine), in September 1961, an abnormal production of long shoots was observed on many young plants of *Chaenomeles* in the Arnold Arboretum. The reaction seemed to be similar in the different cultivars which were affected. As an immediate response, long shoots were produced from adventitious buds located at the base of the shrubs, some reaching 80 centimeters or more three weeks after the application of the weed-deterrent. These shoots were often ramified, but could be distinguished at once from shoots produced after a frost effect by their abnormal leaves and stipules which were, in most cases, extremely narrow and showed discoloration. The leaves appeared variegated and colored pink by anthocyanin pigments. Green pigmentation, chlorophyll, was present in many only along the midribs. These abnormal shoots were especially sensitive to subsequent frosts.

In Cincinnati, Ohio, a very severe attack of seventeen-year locusts occurred in the summer of 1959. In the spring of 1962, *Chaenomeles* shrubs badly damaged three years before were observed at the Stanley M. Rowe Arboretum in different stages of recovery. In many branches the tips were affected so much that they had died back. In such cases, new long shoots were formed from the buds which otherwise would have produced short shoots. Since the branches attacked by the seventeen-year locusts have a tendency to crack open, the living part was often limited to one side. When this happened, all long shoots were produced on this same side, changing radically the ramification which normally alternates along the axis.

Anatomy of the stem. In a young long shoot, a large part of the stem is occupied by pith consisting of round cells containing starch grains. Each of the numerous vascular bundles, distinct at this stage, has a cap of

fibers. The rays are uniseriate. In the cortex, the cells of the ground tissue are loosely arranged and contain chloroplasts and starch grains. The epidermis is brown, as are the simple unicellular trichomes.

In a one-year old stem of *C. japonica*, the trichomes have been shed and a multicellular wart has developed replacing the bulbous base of the deciduous hair. The epidermal layers consist of about four rows of cells arranged tangentially to the axis.

Older stems show a star-shaped pith formed by loosely arranged round cells. The proportion of pith is much smaller in older stems than in young shoots. Diffused through the pith are patches of vertical parenchyma. The uniseriate or sometimes biseriate rays originate in the metaxylem. The annual rings of irregular size are well marked. The wood is diffuse porous but more vessels are formed in the spring. The vessels are usually solitary, or rarely two to three together. The diffuse vertical parenchyma is abundant among the fiber tracheids. The region of functioning secondary phloem is very narrow. The metaphloem consists of a few rows of crushed phloem elements. The protophloem appears as isolated patches of primary phloem fibers. The cortex is formed of 8 to 10 rows of cells tangentially arranged, with many intercellular spaces. Forming the periderm, are the phelloderm, the phellogen, and the phellem consisting of smaller rectangular thick-walled cells, tightly packed together. In *Pyrus*, according to Esau (1953), the periderm originates partly in the epidermis, and partly beneath it. The same is true of *Chaenomeles* in which the wood is very similar to that of *Pyrus*. The cells of the epidermis are light brown in color.

In radial and tangential sections the rays can be observed to be homogeneous, formed of round to oval cells, and non-storied. They can be from 25 to 45 cells high. The vessel elements show simple perforations. The walls are reinforced by spiral thickenings. Between the vessels and the fiber tracheids are alternate to opposite bordered pits. Simple pits are found between the ray cells.

The only specific difference observed in the stems is the difference in growth rate between *Chaenomeles japonica* on one hand, and *C. speciosa* and *C. cathayensis* on the other. For a given stem diameter, *C. japonica* may show twice as many growth rings as the others. *C. japonica* is the only species to show warts on the epidermis of the one-year shoot. The first epidermis is shed during the second year, and after that the stems of *C. japonica* appear as smooth as those of the other species.

Node and petiole. In a long shoot of *Chaenomeles*, the node shows three traces coming from three gaps. In the pulvinus, the two lateral traces divide, one branch of each going into the stipule, the other into the petiole. The three traces inside the petiole fuse together and form one trace along the length of the petiole. According to Howard (1962), this pattern represents three traces from three gaps, with bundles fusing to form a simple arc by simple marginal fusion of the traces. In the pulvinus the petiole has the shape of a half circle. Under the epidermis are one to

two rows of large brown cells, tangentially arranged. The rest is occupied by parenchyma and by the vascular bundle appearing as a smaller half circle in the center with xylem on the adaxial side and phloem on the abaxial side. At the base of the petiole there are no fibers. By the middle of its length, fibers occur in patches forming a broken arc outside of the phloem. Higher up the petiole changes shape as small wings are formed at the adaxial corners. A patch of fibers is found in each wing. In the upper part of the petiole, the traces appear which form the pinnately arranged veins. The first two veins do not leave the midrib at exactly the same point. One appears first, then the other, followed rapidly by the third and the fourth veins on alternating sides.

Unicellular trichomes are occasionally found on petioles, and are a regular feature on the midribs of *C. speciosa* and on the abaxial surface of *C. cathayensis*. In contrast to *Cydonia*, there are no glands on the petioles of *Chaenomeles*.

Leaves and stipules. In *Chaenomeles*, the leaves offer excellent characteristics for distinguishing species (FIG. 4). *C. japonica* possesses obovate to spathulate leaves often terminated by an indentation, and coarsely crenate on the margins. In contrast, the leaves of the other two species are serrate. In *C. cathayensis*, the leaves are elliptic to lanceolate, finely and sharply serrate, each serration terminating in an awn-like tip. *C. speciosa* has ovate to oblong, sharply serrate leaves. The type and amount of pubescence is a characteristic of the species, and is as useful as the serration for recognizing the parents of a hybrid. In *C. japonica*, the leaves are usually completely glabrous, even when unfolding, and only rarely have a few short hairs on the midrib of the under surface. *C. speciosa* is usually pubescent on the midrib of the under surface (exceptionally so on the upper one). *C. cathayensis* has leaves often completely covered, when young, by a fulvous tomentum underneath but when the leaves expand, the tomentum may become thinner or fall off. *C. cathayensis* var. *wilsonii* (Rehd.) Bean, was based on the presence of this tomentum, which in reality occurs in variable abundance in individual adult plants.

In transverse section the leaf shows a normal bifacial structure. Under the epidermis of the adaxial side, are two to three rows of palisade cells above the spongy parenchyma. The vascular bundles are surrounded by a bundle sheath consisting of parenchyma cells. Stomata are restricted to the lower epidermis. The guard cells are reniform.

The leaves of *Chaenomeles* are serrate, each serration and alternating indentation ending with a gland. In cross section it can be seen that both phloem and xylem elements terminate just below the tip of the gland. These tracheids are enclosed by bundle-sheath cells. The epithem, a thin-walled parenchyma without chloroplasts, is little differentiated from the spongy tissue. Glands are known to differentiate relatively early in leaf ontogeny and to function for a short time. In *Chaenomeles* they are nearly full size in unrolling leaf-buds. When functioning, the glands are transparent or tinted red by anthocyanins. The secretion can often be observed

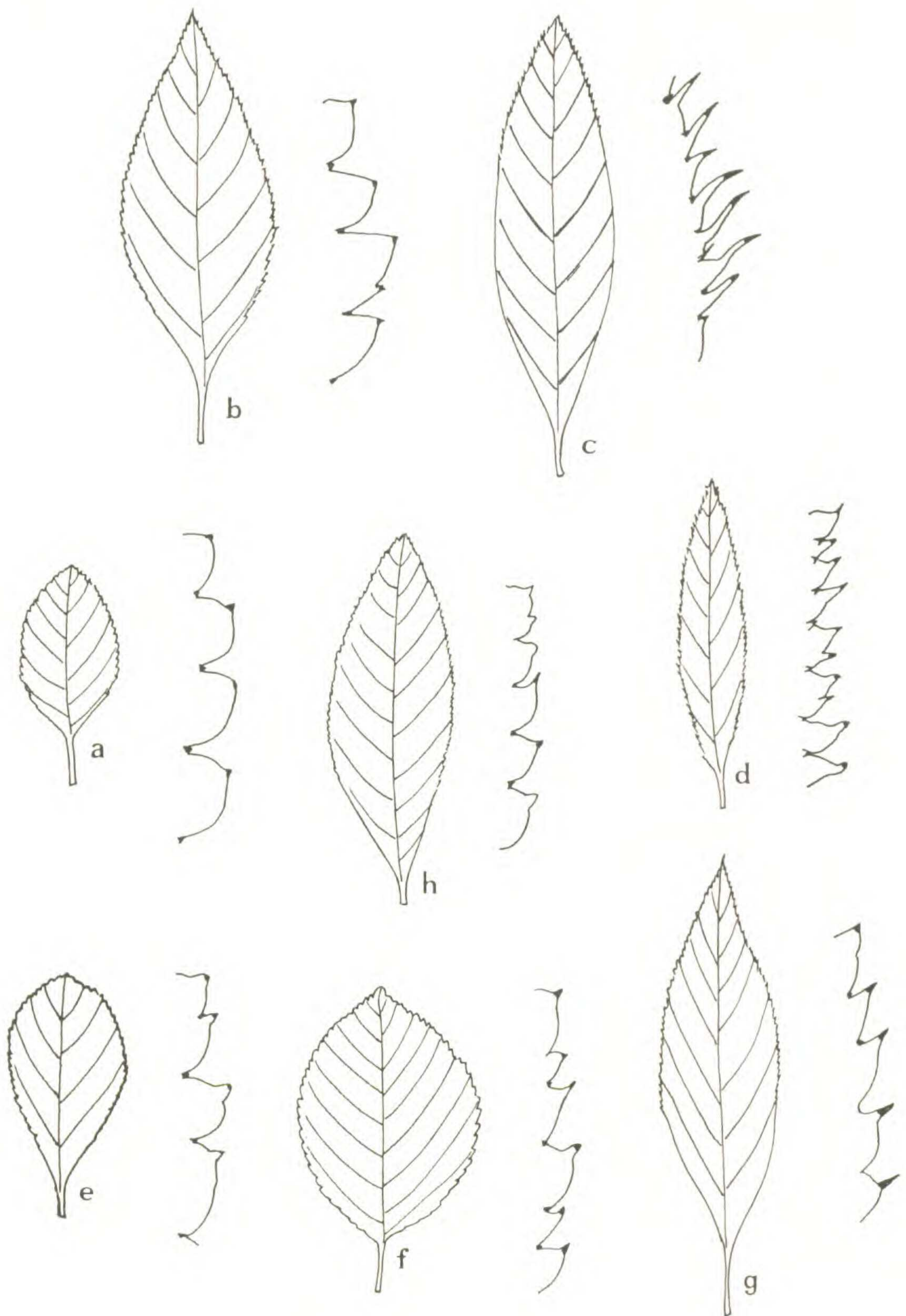FIG. 4. Leaf shape (natural size) and serration types (× 6) in *Chaenomeles*.
a. *C. japonica* 'Sargentii'; b. *C. speciosa* 'Baltzii'; c and d. *C. cathayensis*, c.
leaf from an old shrub, d. juvenile leaf; e. *C × superba* 'Superba'; f. *C.×
clarkiana* 'Minerva'; g. *C. × vilmoriniana* 'Afterglow'; h. *C. × californica* 'Rose-
mary'.

as dried transparent droplets on herbarium specimens. The foliar nectaries in *Chaenomeles* may be considered intermediate between hydathodes and glands by their position, their structure, and their relatively fluid secretion. As soon as the leaves mature and become coriaceous, the glands cease functioning and dry up according to Ono (1907). They appear dark-red or black on adult leaves.

Leaves on short and long shoots were compared in order to find if there were any morphological differences. The leaves have the same shape, type of serration, abundance of glands, and petiole length. Short shoot leaves may be larger than long shoot leaves appearing on the crown, but long shoot leaves of adventitious shoots or sprouts are the largest of all. The leaf size is so variable that it may vary ten-fold in one short shoot. Size and shape could not be used to distinguish isolated leaves as to origin on either long or short shoots. The only difference is the presence on leaves of long shoots of large paired stipules, and their absence on the leaves of short shoots.

The stipules are free, reniform, and show the type of serration and pubescence characteristic of the species. They vary in direct relation to the leaves, tending to be very sharply serrate when accompanying juvenile sharply serrate leaves, or nearly entire in some old shrubs of *C. cathayensis*. Occasionally, stipules have been found to be slightly lobed in three cultivars of *C. speciosa,* 'Alba Cincta', 'Shirataum', and 'Versicolor'.

In *Chaenomeles* the stipules are foliaceous and have palmate venation. A branch of the lateral trace of the petiole goes into each stipule. This divides rapidly into three or five bundles of uniform size. The epidermis is not as resistant as in the leaves and tears off easily. The reniform stipules have a bifacial structure with two rows of palisade cells on the adaxial side. The minor vascular bundles forming a reticulate pattern are located between the palisade cells and the spongy parenchyma, close to the abaxial surface. The bundle sheath consists of parenchyma cells, but only three or five veins possess a bundle sheath extension. The glands, stomata and trichomes are comparable to those of the leaves.

Critchfield's theory (1960) on leaf dimorphism in *Populus* finds application in *Chaenomeles* where dimorphism is expressed in the absence or presence of stipules. Critchfield found in *Populus* that a first type called "early leaves" laid down in the leaf buds in the fall and existing during the winter as embryonic leaves will be produced on short shoots and possibly at the base of long ones. The second type which spent the winter as leaf primordia will appear on adventitious shoots and upper parts of long shoots of the crown. He observed three types of shoots, one with only early leaves, corresponding to short shoots; the second with early and late leaves corresponding to long shoots; and a third type with only late leaves, found in adventitious shoots.

The same situation is encountered in Japanese Quinces. If there is an interruption between the development of short shoots and the start of the long shoots, the number of leaves (4 to 8) observed as embryonic in the bud will all be found fasciculate at the same level, and without stipules.

The production of stipules will start abruptly with the first alternate leaves of the young long shoot. When the long shoot develops without interruption, the first leaves, exstipulate, are alternate along the shoot. It is only when the supply of leaves (maximum 8) which spent the winter as embryonic leaves in the buds has been exhausted, that the leaves with stipules start to be produced. The production of all exstipulate leaves in a fascicle, or their successive production along an axis, is certainly dependent on the weather.

It is not known why stipules are produced only in long shoots, but this may be observed in *Pyrus, Malus,* and *Cydonia* which have less showy stipules than *Chaenomeles,* and also in *Platanus,* a member of the same order, the Rosales. Stipules are also always present in long shoots developing from adventitious buds, and in seedlings.

In *C. cathayensis* the juvenile leaves differ markedly from the leaves produced on adult shrubs. The juvenile leaves and their stipules are smaller, more sharply serrate, always glabrous, and so narrow as to look nearly linear. Their length can be as much as seven times greater than their width, compared to three to four times in the leaves of adult shrubs. It is not known how many years juvenile leaves persist in a plant which originated from seed. A shrub of *C. cathayensis* which germinated in 1936 at the Arnold Arboretum, and has been repeatedly killed back by frost every year, is still producing juvenile leaves on the sprouts it sends up each spring. In contrast, mature leaves can be obtained by grafting a scion of an old plant on a young understock. In *C. cathayensis,* mature or senile leaves often appear subentire and show a thick tomentum on the under surface.

The juvenile leaves of *C. japonica* and *C. speciosa* do not differ markedly in shape from their mature leaves, but are only slightly smaller. In *C. japonica,* the teeth of the crenate leaves are evident at a later stage than the fine serrations of the other two species. It is probably a case of allometric growth, since crenate and serrate leaves look alike during the embryonic stage in a bud or in a young seedling.

The foliage, as recorded in the last three years, appears during the last week of April, or more often the first week of May, in the climate of Boston. The first flush of growth during the blooming period produces fasciculate leaves on short shoots. These are nearly always green. By the middle of May to the middle of June the long shoots elongate. Their leaves are very often brightly colored pink or brown from an abundance of anthocyanin pigments. The coloration extends from the midrib toward the extremities of the veins, and the chlorophyll appears as green patches isolated in the reticulate red pattern. One cultivar at least, *C.* × *superba* 'Foliis Rubris' has been named for its red leaves. In spite of its name, the foliage coloration does not last any longer than in other cultivars. The cultivar which probably retains the red pigmentation longest is *C. speciosa* 'Kermesina Semiplena'. By the middle of July the foliage of all the Japanese Quinces appears glossy green and remains so for the rest of the season, except at the growing tips of the shoots.

Leaves of *C. japonica* and *C.* × *superba* are often a yellow-green, while *C. speciosa*, *C. cathayensis* and the other hybrid groups usually possess leaves dark green on the upper surface and lighter below. Two cultivars have been named for their variegated foliage, *C. speciosa* 'Foliis Variegatis' and *C. japonica* 'Tricolor'. *Chaenomeles japonica* 'Tricolor' which is still in cultivation shows leaves of three colors, pink, green, and white, on the new long shoots. Mature leaves are green or variegated green-and-white. An albino mutation was observed by Simirenko (1888) on a branch of *C. speciosa* in which all the leaves were white, without chlorophyll. Simirenko named it 'Simirenkiana' and grafted it on normal understock in order to produce Japanese Quinces with white leaves. On this branch the flowers were also of a lighter shade than on the rest of the shrub. The fate of this "cultivar" is unknown.

In areas with dry hot summers Japanese Quinces may lose some of their leaves in midsummer. Some nurserymen suggest that by removing the fruits, or growing cultivars with weak fruit production, defoliation will be prevented. This fact is contested by other horticulturists, and has not been proved one way or another. Chlorosis has been observed on *Chaenomeles* growing in lime soils.

In the autumn the leaves fall gradually, being mostly gone by November 10. There is no fall coloration of any kind, unlike most species of *Cydonia*, *Pyrus*, and *Malus* which color brightly in red, or at least tint with yellow, before falling. In warmer climates *Chaenomeles* is reported to have nearly persistent leaves.

As observed, the leaves, especially when young, are less resistant to cold than the flowers. With a late frost in the spring leaves can be damaged, appearing crinkled when unfolding, although the flowers are not touched.

Inflorescences. Along with the tendency to flower at any time of the year, weather permitting, *Chaenomeles* presents a great variety of inflorescence types. A few cultivars have been named for their long peduncles, such as *C. speciosa* 'Pedunculata'. These pedunculate inflorescences appear on any shrub if heat, light, and humidity are sufficient. They are not a varietal character, but rather a seasonal phase.

In *Chaenomeles*, the inflorescences vary from one to six subsessile flowers appearing together at one point, to a very elaborate raceme or panicle, sometimes including leaves, stipules, and bracts. A correlation with the short and long shoots may explain what kinds of responses are brought about by the environmental conditions. The different inflorescences, modifications of cluster, spike, raceme or panicle, which can be found on any one shrub are of two main types, one being analogous to a short shoot, the other to a long shoot. An intermediate type is sometimes observed.

The *short shoot* type is found in the spring and in the late fall (FIG. 5 a; FIG. 6 a, 6 e). Its flowers have spent months in an advanced embryonic state in an open bud. They are clustered, (1) 2 to 6, on old wood or on the long shoots of the preceding year. The flowers have extremely short

FIG. 5. Inflorescence types (natural size). a. Spring inflorescence, with short pedicels, of *C.* × *californica* 'Arthur Colby' (May 4); b. fall inflorescence of *C. speciosa* 'Phylis Moore' (October 2); c. summer inflorescence of *C. speciosa* 'Phylis Moore' (May 28).

or non-existent peduncles, and no bracts. This is the normal type of inflorescence at blooming time in early spring, before the leaves appear. If branches are lying on the ground partially buried in mulch, the flower buds will develop in the same manner, but the peduncles will expand in order to reach the surface. In any case, each flower peduncle will be distinct from the others.

Flower buds are formed very early. If the cold weather does not set in, flowers which were prepared for the following spring start to open in late fall. It is difficult to tell whether the inflorescence type consisting of a few sessile flowers, fasciculate at one node, is brought about by a return of the early spring conditions of temperature, humidity, short days, and absence of leaves, or whether it depends, as in short leafy shoots, on the advanced embryonic condition of the flowers in the buds.

An intermediate situation between short and long shoots has been observed several times in living plants as well as on herbarium specimens. The bud produces a short shoot during the spring like any other short shoot. It is continued, sometimes without interruption of growth, by a slightly branched cluster of three to five pedunculate flowers. No leaves, stipules or bracts are produced and the whole inflorescence is not more than two to five centimeters long. Normally, a short shoot does not elongate and forms a bud at the end, often destined to produce flowers the next spring. For an unknown reason these flowers develop the same season. This intermediate condition may be found in late spring and in early fall (FIG. 6 b).

The *long shoot* type of inflorescence occurs from late spring to late fall. So far, it has not been possible to predict where and when summer inflorescences are going to appear. At this time, the shrubs are covered with leaves. Summer inflorescences, like sprouts, develop very fast if the temperature is favorable. When they can be recognized, it is too late to find out in what kind of embryonic condition they spent the winter. This can be deduced by their location, often on old wood, even on the main branches, and also by the fact that at this time of the year there are only rudimentary dormant buds. Summer inflorescences, like the long leafy shoots, probably spend the winter in a primordial stage.

The peduncle length appears to be dependent on the temperature, a few degrees change at night probably being enough for change from a spike to a raceme or a panicle. The variation in long shoot type of inflorescence is even more striking, involving the presence or absence of leaves, stipules, bracts, or intermediate organs, as well as the transformation of the sepals into leaves. This type of inflorescence is extremely variable and may be subdivided into four categories.

1. A few exstipulate leaves are found at the base or along the axis. They are succeeded by leaves with small stipules. Axillary to each leaf is a flower or a ramified branchlet with two or more flowers associated with bracts. The shoot is terminated by a flower. Unbranched, it may be a spike or a raceme, when branched, a panicle. It may reach a length of 20 centimeters in a few days. This is the commonest inflorescence type in the summer and occurs from late spring to fall (FIG. 5 c).

2. In a variant of the preceding the leaves, usually not more than six, lack stipules. The flowers may occur in the axils of the leaves or above them. Bracts are usually absent. This type is common in the fall. The inflorescence may reach 20 centimeters or more (FIG. 5 b).

3. A third and infrequent type of inflorescence may be formed in the fall. A

FIG. 6. Inflorescence types (natural size). a. Spring inflorescence, with long pedicels, of *C. × superba* 'Perfecta' (May 10); b. intermediate inflorescence of *C. speciosa* 'Simonii' (June 25); c. fall inflorescence, with heart-shaped bracts and foliaceous sepals, of *C. japonica* 'Sargentii' (November 10); d. inflorescence appearing through the ground, of *C. japonica* 'Sargentii' (June 6); e. late fall solitary flower of *C. speciosa* 'Simonii' (November 17).

few exstipulate leaves are laid down at the base. The whole shoot ramifies and heart-shaped, serrate organs, intermediate between leaf and stipule, are found in place of the usual inconspicuous bracts. This modification is carried out to the

calyx which becomes foliaceous. These leafy bracts and sepals bear glands on each tooth. It is not known if they ever secrete any liquid (FIG. 6 c).

4. In two instances, in summer and early fall, inflorescences were found coming up through the ground. One was formed on a very old shrub of *C. japonica* 'Sargentii', and the other, on a young plant of *C. × superba* 'Elly Mossel'. The shoots elongated through the ground, without bearing any leaves. Once in the open they developed bracts, some normal, others heart-shaped, then flowers with foliaceous glandular sepals (FIG. 6 d).

Sometimes there are other abnormalities accompanying foliaceous bracts and sepals such as glands appearing away from the edges (on the adaxial side only, and always connected with veins), stamens transformed into petals or sterile styles with extra branches, and so forth.

At least some of these different types of inflorescences are common and usually appear at the same season year after year, probably as a response to similar environmental conditions. They cannot be associated with any particular species or cultivar. On one shrub of *C. japonica* 'Sargentii' which originated from seeds brought back by Sargent from the mountains of Japan, six of the seven types and subtypes have been observed during the last two years. Summer inflorescences are so frequent that not only cultivars, but also botanical species or varieties have been named for these seasonal phases. The type of *C. speciosa* (Sweet) Nakai, an illustration, plate 692 in the Botanical Magazine, represents an inflorescence intermediate between a short and a long shoot. The syntypes of *C. japonica* var. *pygmaea* Maximowicz are specimens, collected in flowering condition in December, of the short shoot type with long peduncles, appearing exceptionally in late fall. Other characteristics which vary according to the temperature were included in the original description.

The different types of inflorescences found in *Chaenomeles* at different times of the year encompass the range of inflorescences found in the closely related genera. Since these genera have a limited blooming period, only one type of inflorescence occurs which is considered characteristic of the genus. *Docynia* possesses a few clustered subsessile flowers. They are analogous to the spring inflorescences of *Chaenomeles*, and comparable to those of short shoots. *Malus* has the short shoot type of inflorescence with long peduncles. *Pyrus*, also some species of *Malus*, present the intermediate situation with fasciculate leaves and a slightly branched, but short and naked inflorescence in the center. This has been called "pyrostele" by Bailey (1949a) who thought that this type was peculiar to *Pyrus*. This term is unfortunate for the confusion it can cause with the anatomical meaning given to the term stele. *Cydonia* possesses solitary flowers occurring at the tips of leafy shoots. This inflorescence is a typical modification of a long shoot, which in *Chaenomeles* ends up with a spine, or is modified into a branched inflorescence. The different types found in these four genera develop at the same time as the corresponding types in *Chaenomeles*. Consequently, they must not be considered as genetically determined, but rather as arising in physiological response to the environment.

Flowers. The variation in inflorescences found on any one shrub is matched by an equal or greater variation found in the flowers. Normally, flowers are produced from special buds, early in the fall. In the spring, flowers open within a few days in good weather. They usually open before the leaves, but the leaves develop and start to unfold when the petals are still present. The aestivation of the sepals and petals is imbricate, as in *Pyrus* and *Malus*, and in contrast to the contorted condition in *Cydonia*.

The hypanthium forming the base of the flower varies from cup-shaped to gourd-shaped. There is a tendency for the hypanthium of *C. japonica* to be more nearly cup-shaped; for *C. speciosa*, more gourd-shaped; and for *C. cathayensis*, to have an elongated hypanthium. Moreover, the shape of the hypanthium is complicated by the presence of numerous unisexual flowers in every species, which are more nearly cup-shaped when entirely male, more nearly gourd-shaped if entirely female. This does not always hold true, for flowers with long hypanthia sometimes have no ovules, and flowers with short hypanthia may have ovules which appear superficially to be borne in the peduncle. The receptacle, formed of the hypanthium and prolonged by the 5 sepals is always glabrous. It is woolly or at least pubescent in *Cydonia*, *Docynia*, and *Pyrus*. In *Chaenomeles* the receptacle is often brightly colored purple or brown on the sunny side, by anthocyanin pigments.

The sepals appear as five short truncate or round, ciliate lobes, without glands, but pubescent inside at the place where the petals are attached. The lobes, often unequal in size, are always erect at anthesis. In contrast, the sepals are reflexed in *Cydonia* and *Pyrus*, and are glandular in *Cydonia* and *Docynia*. The calyx lobes, as well as the hypanthium of which they are a prolongation, are very much vascularized by anastomosing traces. The sepals are ciliate with single unicellular trichomes.

Sepals can show two abnormalities. They may either become leaf-like, a relatively frequent condition, or more rarely, petal-like. Foliaceous sepals occur normally on at least two types of inflorescences, and in this case, they are serrate and glabrous on the edge, each serration being terminated by a gland. They are pubescent inside, as usual. If only partially leafy, the entire edge will be ciliate, and the trichomes are abruptly replaced by glands where the serrations begin. A partial development of petal-like sepals is sometimes found. This latter case is of common occurrence in *C.* × *superba* 'Texas Scarlet'.

The genus *Chaenomeles* normally has five regular, free, slightly unguiculate round petals. They are borne on the hypanthium, opposite the sepals. They may be carinate, especially in *C. japonica* and *C.* × *superba*, undulate, or flat at the end of anthesis. The petals are short pubescent on the claw, glabrous otherwise, and have exceptionally been found to be ciliate and bordered with small capitate glands in *C.* × *superba* 'Crimson and Gold'. The petals possess slightly larger cells than the sepals, and are less vascularized. At least three traces enter each petal. They divide dichotomously and the veins anastomose to form a reticulate pattern often reaching the edge of the petal.

Petals are never less than five, but when broad and overlapping the flowers appear semidouble, even with a regular number. Often, there are more petals from a partial modification of stamens and the number may reach 15 which are quite variable in size and shape. Numerous cultivars with semi-double or double flowers have been named. This character may vary widely, flowers being double on a young shrub, or when the number of flower buds has been reduced by frost, single when the shrub is older and loaded with flowers. Isolated summer flowers often have a greater number of petals than spring flowers.

The genera *Cydonia* and *Chaenomeles* are cited as having petals which drop before wilting. They do so after four or six days, even before the outer stamens have shed their pollen, if the weather is hot. A longitudinal section of the flower reveals an abscission layer formed between the hypanthium and the petals. On both sides of this constriction the cells are smaller and more tightly packed. The abscission of the petals which are shed when perfectly turgid occurs at this constriction. The separation seems to start from the center and proceed toward the outside. Since stamens do not possess an abscission layer, petals on double flowers are not shed, and can often be seen to persist on young fruits. The double flowers last considerably longer than the single ones.

The petals of *Chaenomeles* cultivars can show a great array of colors, from white to darkest red, through all shades of pink, orange, and scarlet. Bicolored petals are also frequent. The color intensity and petal size are in direct relation to light, and probably to heat. In rainy spring seasons, flowers appear pale and dull. This relationship is also obvious from an observation of the flowers borne on one shrub from early spring to late fall. The color becomes more intense until August and September, reverting later to lighter shades. Very few cultivars are pure white during the summer months. The effect of light may also be observed by comparison of flowers opening at the same time on the outside and inside of a leafy shrub, or on double flowers in which the parts where the petals overlap remain uncolored.

Most cultivars have been selected and named on the basis of petal color. A classification of cultivars according to their color can only be approximate, due to the changes in intensity throughout the year. In addition to the weather, the soil may have an influence. Nakai (1916) is the only botanist who attempted to distinguish species by the color of the flowers alone. He raised *C. speciosa* var. *eburnea* to the rank of species and placed in it all the cultivated varieties with white petals.

As a reverse case from petaloid sepals, sepaloid petals may also be found. *C. speciosa* 'Simonii', with semidouble flowers, has outer petals often marked with a green line, the red colored parts appearing as two wings. The sepals of this cultivar are normal.

The stamens, 40 to 60 in number, are borne on the hypanthium below the petals, more or less in two rows. They are free and shorter than the petals. The filaments are glabrous, white or pink or dark rosy-red when developing in summer conditions. The anthers are introrse, basifixed at

first, becoming slightly versatile when old. They are yellow, turning to brown after the pollen has been shed. The extra petals in semidouble and double flowers are modified stamens which may retain one or more anther sacs on the edge. All transitional stages between stamen and petal can be found.

There is no constriction at the base of the stamens, rather a slight enlargement. The tissue of the hypanthium with its large cells arranged vertically continues without interruption into the filament up to the anther. There is one trace only entering the filament. The few protoxylem elements which form the vascular bundle show reinforcement by spiral thickenings. The center of the vascular bundle is often hollow. The vascular bundle stops at the base of the anther sacs, but diffused protoxylem elements may be found in the connective. The epidermis of the filaments, formed of very small cells, is cutinized. Stomata have been observed, but there are no trichomes present. Under the epidermis is another row of slightly larger cells around the ground tissue.

The anthers, in an early stage, show two lobes and four locules. Close to maturity the anthers have two locules only, by loss of the partition within each anther half. Beneath the epidermis is the endothecium which consists of large cells, tangentially arranged, their walls, except the one in contact with the epidermis, being reinforced by conspicuous secondary wall thickening strips oriented perpendicularly to the epidermal layer. There is an interruption of the epidermis and of the endothecium at the place where dehiscence will occur. The stomium is a longitudinal slit located between the locules of each half of the anthers. Before opening it is plugged by a chain of very small thin-walled cells. Just before dehiscence starts, the parietal layers inside the endothecium and the tapetum disintegrate and appear as collapsed or crushed cells.

In the double flowers, some of the stamens are petaloid. In longitudinal section, it may be seen that in spite of their change of function and color, they have a single vascular trace, and lack trichomes completely at the base. This sole trace divides much higher up in the claw and eventually produces a normal reticulate vein pattern. A fragment of anther is often retained, with or without pollen production. There is neither constriction at the base, nor small cells arranged tangentially to interrupt the tissue of the hypanthium. This explains why "petals" of double flowers do not shed as in single flowers. The outer or normal petals of double flowers do possess a constriction and are shed unnoticed, while petaloid stamens persist until the abscission of the top of the hypanthium occurs a few weeks after pollination.

Functionally female flowers are formed by the abortion of stamens and are less common than functionally male flowers. Although they are not recorded in the horticultural literature of *Chaenomeles*, functionally female flowers occur occasionally in many shrubs, or very frequently in such cultivars as *C.* × *superba* 'Alba Semiplena', 'Columbia', 'Early Apple Blossom', and 'Sunset'. Two shrubs of 'Columbia', grown side by side, have been observed for a few years to produce female flowers only. In the

spring of 1963, they both produced a few male flowers and no female ones. In these female flowers, stamens in reduced number were present but did not contain any pollen and often the anther sacs were transformed into pink appendages in the shape of horns.

The pollen grains of *Chaenomeles* are tricolpate, without ornamentation; the three germ pores are evident at the rounded corners. The exine between the pores is thick and smooth. In herbarium specimens of wild and cultivated plants, the pollen grains measure from 25 to 55 micra. There is a great variation in size of pollen grains coming from the same anther. The three species and their hybrids have been found to have pollen grains with the same range in size. The greatest variation in pollen size has been observed in a specimen of *C. japonica* collected in Japan. The grains measured from 15 to 32 micra. The pollen of the cultivars representing the interspecific hybrid groups has been found to be on the lowest part of the range, while the pollen of *C.* × *californica* 'Clarke's Giant Red', a tetraploid, was in the upper part of the same range. These measurements do not seem to be significant since the variation is so great in the pollen contained in one anther, and is no larger in cultivated plants or in hybrids than in wild plants. It is impossible to recognize the species or the genus by the pollen. The two species of *Cydonia* have similar pollen, also within the size range of *Chaenomeles*.

The proportion of bad or empty pollen grains which do not stain with aceto-carmine can be from $\frac{1}{10}$ to $\frac{1}{4}$ of the total. The proportion of empty pollen has not been found to be significantly different in hybrids and in species, or in cultivated specimens and in wild specimens. It varies a great deal on the same shrub at different dates, and seems to be dependent on weather conditions.

Between the inner row of stamens and the column formed by the fused styles, is a glabrous, nectariferous interval called a disc. The disc is larger in male flowers when the column formed by the styles is reduced in size or absent, than in predominantly female flowers. The disc covers the part of the carpels fused to the hypanthium and is the place where nectar is excreted. The epidermis of the nectary appears no different from that of the rest of the hypanthium. Beneath the epidermis, a nectariferous zone is several cells thick and extends in the form of a network. It consists of very small round cells, closely packed and staining differently from the ground tissue. When the cell content persists, it shows numerous small refringent granules. The floral nectaries differ anatomically from the leaf glands in lacking vascular bundles.

The column formed by the styles is characteristic of *Chaenomeles*, although it may vary widely within one species. The styles may be completely fused, in which case the column is solid, or partially fused, forming a hollow column. At the base are some straight unicellular trichomes which may vary from abundant to entirely absent. Trichomes are occasionally found within the hollow columns. Each style is vascularized by two to four traces. The ground tissue consists of large cells longitudinally arranged, and bordered by an epidermis. The styles are always free above.

The decurrent stigmata have a glandular papillate epidermis. The stigmatoid tissue of large and longitudinally arranged cells forms anastomosing strands connecting the stigmata to the ovules. These cells stain in the same way as the nectariferous cells, and also possess refringent granules. In longitudinal sections, the stigmatoid tissue may be observed very close to the reticulum formed by the nectariferous tissue. The two kinds of cells may be distinguished by their size.

The five styles in *Chaenomeles* are fused for ⅓ to ⅔ of their length. This is a generic character not present in the related genera which have free styles coalescent by the hairy covering. The column is commonly glabrous or glabrescent, less often pubescent, rarely woolly. It is always glabrous in *C. japonica*, pubescent to woolly in *C. cathayensis*, and varies from glabrous to woolly in *C. speciosa*, with the greatest number of cultivars being glabrous or glabrescent. Japanese authors put much emphasis on this character and still recognize Nakai's (1916, 1918, 1923, 1929) four "species," separated according to the pubescence of the stylar column: *C. eburnea*, glabrous; *C. speciosa*, glabrescent; *C. trichogyna*, villose; *C. extus-coccinea*, woolly. Nakai himself (1929), gave as synonym of *C. extus-coccinea* with a woolly column, the cultivar 'Alba Cincta' (as *C. japonica* var. fl. *roseo, albo-cincta*) which has a glabrous column. Such variation in the pubescence of the column is not correlated with other morphological characters. The part where the styles are free is always glabrous. The styles are white, exceptionally red (observed in summer flowers only). They terminate in green decurrent stigmata, comparable to those of *Cydonia* and *Docynia*, but contrasting with the discoid stigmata of *Pyrus* and *Malus*.

Many aberrations may take place in the styles. Often more than five styles, and up to nine, have been observed in the same flower. They usually correspond in number to the carpels, but extra styles may also occur by branching just under the stigmata. These extra branches are often found in flowers appearing in the fall. In some cultivated shrubs of *C. speciosa*, the styles are abnormal year after year. In a few flowers, they are fused into a hairy cone protruding above the petals. These flowers appear to have a superior ovary, in contrast to the normal inferior ovary of the Maloideae.

In other and common instances styles may vary from normal size, about ¼ longer than the stamens, to being completely absent. Every transition has been observed in the flowers of a single shrub, which can produce normal hermaphrodite flowers with long styles, others with styles of the same length as the stamens, some shorter, as well as flowers which are completely male by abortion of the female organs. Flowers are found with ovules and no styles or with normal styles and stigmata, and no ovules. In contrast to functionally female flowers which always contain sterile stamens, male flowers usually do not have styles or ovules. Contorted styles of normal size, but without stigmatic surface are extremely rare. Male flowers are very common, even in wild specimens. The syntypes of *Chaenomeles japonica* var. *pygmaea* Maxim. show male flowers only. So

does plate 692 of the Botanical Magazine which is the type of *C. speciosa* (Sweet) Nakai.

Under the disc are found the five carpels. They are completely fused to the hypanthium on the abaxial side, and fused together on the adaxial side. They form an inferior syncarpous ovary with five locules, but numbers from three to seven have been observed. Carrière (1876b) found a fruit in which the five carpels gave rise to ten locules by the production of false partitions perpendicular to the normal ones. Exceptionally, carpels are incompletely fused in the center (as in *Cydonia* and *Docynia*).

A transverse section through the ovarian region shows a cutinized epidermis formed by small cells without trichomes. Directly beneath the epidermis are two to three radially oriented rows of collenchymatous tissue of larger tightly packed cells. The ground tissue forming the bulk of the hypanthium and of the carpels, consists of large cells loosely arranged. Immediately internal to the collenchymatous tissue are numerous small vascular bundles forming an irregular circle. Near the inner side of the hypanthium are ten vascular bundles which vascularize the sepals and the petals. At the tip of each of the five carpels is another vascular bundle. Between the two circles is the boundary of the ovary and the hypanthium. These two organs are completely fused in *Chaenomeles* and are anatomically indistinguishable. The ground tissue of each is a loose parenchyma. At the time of anthesis there are no sclereids in either of them. However, only the ovary tissue has the strands of stigmatoid tissue. Each locule contains about 20 anatropous ovules with two integuments, arranged horizontally in two rows.

Fruits. The fruits of *Chaenomeles* are pomes as in the other Maloideae. There are two conflicting theories as to the interpretation of the inferior ovary in the Maloideae. The usually adopted one is the Axial Theory of the nature of the inferior ovary, also called the Receptacular Theory. In this theory, the hypanthium is considered basically axial, consisting, according to Eames (1961) of the rim of the receptacle. Under the Appendicular Theory, however, the hypanthium is considered to consist of the adnate bases of sepals, petals and stamens. Most authors commonly cite the Maloideae as showing inferior ovaries in which the receptacle has a prominent part. Eames, through comparative studies of the floral anatomy of the Rosaceae, and comparisons of proliferated rose and apple fruits, arrives at the opposite conclusion. For Eames, the fleshy outer part of the apple and the pear consists morphologically of the fused bases of appendages. The fruits of *Chaenomeles* in which the calyx lobes often persist and become accrescent, forming the upper part of the fruits, seem to accord with the Appendicular Theory.

The transformation of the ovary and the hypanthium into a pome occurs in the same manner as in the apple, which has been studied by several authors. The ripe fruit is brightly colored yellow by chromoplasts. The cuticle on the outer side has thickened; it may become sticky in some cultivars. The stomata have been transformed into lenticels consist-

ing of patches of suberized cells. In some fruits, patches of suberized cells occur also at random on the skin, especially near the apex. This corresponds to a phenomenon called "russeting" in apples where the outer layers of the fruits are replaced by cork (Tetley, 1930). The subepidermal parenchyma consists of several layers of tangentially elongated cells, which contain carotenoids. These cells were radially oriented in a cross section of the flower. They have divided and enlarged and by a difference in allometric growth, have changed their orientation. Their walls also have thickened, and they are as tightly packed as earlier, in contrast to an apple whose tissues become relatively soft at maturity. The fragrance as well as the coloration of the fruit appear to be localized in the epidermis and in the subepidermal parenchyma. The ground tissue is of loosely arranged parenchyma, well vascularized by a network formed by the anastomoses of the main traces. In a young fruit, the parenchyma cells contain chloro- and chromoplasts. Chloroplasts degenerate at ripening time, and carotenoids are present, but in lesser quantity than in the epidermis and subepidermal layer. In spite of the fact that the fruits of *Chaenomeles* do not soften in ripening, there are many intercellular spaces between the large more or less radially oriented cells of the parenchyma. The fleshy part of the fruit which corresponds to the hypanthium tissue is the exocarp.

In a young ovary, the limit between the hypanthium and the carpels was undiscernable between the circle of ten traces going to the sepals and petals and the circle of five traces on the dorsal side of the carpels. In a mature fruit, patches of sclereids have developed around the median and lateral vascular bundles at the limit of the floral tube and the carpels. These patches become confluent and form an irregular ring of sclereids. There are no sclereids in the flesh of *Chaenomeles* nor are there any in *Malus*. In contrast, there are patches of sclereids or stone cells in the ground parenchyma of the fruit of *Pyrus, Cydonia,* and *Docynia.* Inside of the circle of sclereids are the carpels which became cartilaginous early in the development of the fruit. They also are strongly vascularized and possess sclereids. This is considered to be the endocarp lining the locules (McDaniels, 1940). In *Chaenomeles,* the carpels are usually completely fused in the center.

The fruits present a great variation in their shape. More commonly, they are apple-, orange-shaped, or ovoid, when coming from spring flowers; pear- or fig-shaped, when formed on summer or fall inflorescences. Morren (1851) has also observed fruits of *C. speciosa* in the shape of a falciform and ribbed zucchini. As a rule, fruits of *C. japonica* are small and apple-shaped; fruits of *C. cathayensis* are large and ovoid; fruits of *C. speciosa* and of the interspecific hybrids vary in shape and size. A few cultivars (e.g. 'Citri-pomma', lemon-shaped; 'Pyriformis', pear-shaped) have been named for the shape of their fruits. In continental Europe, summer flowers on *Chaenomeles* are infrequent, and have attracted the attention of botanists when they appeared. In New England, where they are of common occurrence, pear-shaped or fig-shaped pedunculate fruits

are found every year on many shrubs. Instead of appearing isolated on
old wood, they are clustered on a ramified young shoot. They usually
contain fewer ovules than spring fruits, and never mature, being killed
by frost.

Independent of their shape, fruits are smooth or ribbed in a few culti-
vars. Usually there are ten ribs in *C. speciosa* 'Grandiflora Rosea',
'Kermesina Semiplena', 'Phylis Moore', 'Simonii', 'Spitfire', and *C.* ×
superba 'Knap Hill Scarlet'; and only five ribs in *C.* × *superba* 'Ulidia'.
This character of having ribs is constant in a cultivar and occurs in fruits
formed from spring flowers as well as in fruits formed in the summer and
fall.

The fruits of *Chaenomeles* have another peculiarity not found in the
closely related genera. They very often terminate in a prominent umbilicus.
Other times the calyx becomes accrescent and protrudes as a fleshy rim
above the fruit, or it dries up and may persist with the stamens (as in
Malus, *Pyrus*, and *Cydonia*). The three different kinds of apices may
occasionally be found in the fruits of the same shrub. However, the fruits
usually offer good characteristics for recognizing some of the cultivars.
As the flowers of *Chaenomeles* are similar in all three species, it is inter-
esting to determine the development of these different shapes of fruits.

A swelling of the ovary is evident 10 to 12 days after anthesis. When
cut open longitudinally it may be observed that the center where the
carpels are fused has increased considerably, and that the ovules have
started to enlarge, while the hypanthium is of about the same width as in
the flower. At this time there is a natural thinning of the fruits. The
flowers which are not pollinated, and certainly many others, fall off. In
these, the ovules, instead of increasing, have by now dried up. Soon after,
the calyx is shed in one piece by an abscission produced below the inser-
tion of the stamens at the constriction occurring in a more or less gourd-
shaped hypanthium. The styles are present and the separated calyx is
sometimes retained for a while as a loose ring surmounting the young
fruit. The fruit continues to increase in girth, more by enlargement of
the center and of the locules than by a thickening of the flesh, which will
take place after the locules are nearly full size.

The shape of the apex of the fruits of Japanese Quinces is determined
in the first few weeks after pollination, by the abscission or persistence of
the calyx, and of the stylar column. The place where the abscission
occurs on the column determines the presence or not of an umbilicus. If
nothing is left of the column, and if the calyx was shed, the fruit will be
terminated by a depression; or if the calyx persists and becomes accres-
cent, by a hollow protuberance. If a few millimeters of the column re-
main in the fruit this narrow base will enlarge and form an umbilicus. It
may remain sunken in the fruit, be hidden under the accrescent calyx,
or be evident by protruding in the cavity left in the hypanthium after its
transformation into a pome. The umbilicus is usually hard and fibrous.
The cultivar *C. speciosa* 'Umbilicata' has been named for having an
umbilicate fruit. Fruits with a very large umbilicus are also found in

C. speciosa 'Fireball' and 'Doctor Bang's Pink', and in *C.* × *superba* 'Incendie'. Umbilicate fruits are common in other cultivars, but the umbilicus is not apparent unless the fruit is sectioned longitudinally. Since the column formed by the fused styles is a characteristic of the genus *Chaenomeles*, it is not surprising that umbilicate fruits do not occur in other Maloideae. Occasionally, a shrub shows fruits of different shapes, a condition first observed by Morren (1861). Irregular or malformed fruits may be caused by abortion of the ovules on one side. Ovules after pollination must produce auxins which govern the growth of the flesh. The grooves always correspond to partially or totally empty locules.

The first part of the pome to develop is the core containing the carpels and the ovules. For flowers which were pollinated during the first week of May the core and the ovules have reached approximately their mature size by the beginning of August. Fruits formed in the summer develop much faster. When the core has become cartilaginous the flesh will start to increase. The stage of cell division described by Clements (1935) is replaced by a stage in which the cells enlarge slowly up to the maturity of the fruit.

The skin of *Chaenomeles* fruit is always very thin and completely glabrous. Some of the interspecific hybrids of *C. japonica* possess characteristically sticky skin, which is also a sign of maturity. The skin remains dry in the other two species. The color of the ripe fruits is yellow. Sometimes the showiness of the fruits is the main merit of a cultivar, as in *C.* × *superba* 'George Landis' with orange fruits. This stage of ripening is not reached by all cultivars in the climate of Boston, for the earlier ones mature usually in October. Fruits of *C. cathayensis* need more heat to show color. If fruits do not ripen they remain green, but often are pink or brown on the sunny side. The ripening is also evident in the fragrance of the fruits. The mature seeds are brown. *Chaenomeles* fruits often fall off all at once, especially after a white frost. The fruits may be ripened indoors and formerly, were kept in closets for their pleasant odor. They remain hard and acid until they decompose.

Spring inflorescences contain as many as six subsessile flowers clustered at one point. By natural thinning the number of fruits is usually reduced, but as many as four mature fruits have been observed at one node. The peduncles did not elongate, and they developed a special shape due to the crowding. In *C.* × *superba* 'Boule de Feu' where the peduncles are completely absent, the fruits often surround the supporting spiny twig. This abundance of sessile fruits in the fall is a special aspect of *Chaenomeles* shrubs. The fruits appear on old wood to the ground level. Fruit production is sometimes very heavy, especially in *C. cathayensis* and in *C. japonica* 'Maulei'. *Chaenomeles japonica* is usually the species maturing first, which may be due to its low stature, as is its hardiness.

Seeds. The numerous seeds are arranged horizontally in two rows, in each of the five locules. There may be up to 120 in *C. cathayensis*, about 80 in *C. japonica*, and an intermediate number in *C. speciosa* if the ovules

are all fertilized and develop. This is usually not the case, and seeds in full sized fruits number not more than 70 to 80. There appear to be fewer seeds in fruits of interspecific hybrids.

The seeds of *C. japonica* and *C. speciosa* are ovoid and pointed at one end, while those of *C. cathayensis* are wedge-shaped. The testa is coriaceous, dark or reddish brown in the first two species; coriaceous or very slightly mucilaginous, light brown and dull in *C. cathayensis*. In contrast, seeds of both species of *Cydonia* are highly mucilaginous. The raphe and chalaza are apical. The endosperm is lacking. Seeds help in recognizing interspecific hybrids, especially those involving *C. cathayensis*. The seeds of *C. japonica* and *C. speciosa*, in spite of being very numerous in each locule, are more or less ovoid (as in *Pyrus* and *Malus*). In *C. cathayensis*, they take a planoconvex shape by compression with each other (as in *Cydonia*).

Seedlings. In *Chaenomeles* the percentage of seed germination is high, and does not appear to be decreased in interspecific hybrids. After a cold period the germination of the seeds takes place immediately. The root ramifies very fast. In five or six days the seedlings, still surmounted by the split testa, begin to emerge above the ground. After shedding the seed coat, the two, rarely three, cotyledons expand and the plumule becomes visible. The young leaves, as well as their stipules, are immediately serrate (also in *Cydonia oblonga*), each serration and interval being marked by a reddish gland, secreting liquid. The glands are sometimes found at a distance of a few millimeters from the edge, on the upper surface of the leaves. The hypocotyl is glabrous while the epicotyl is pubescent.

One or two weeks after germination the seedlings of different species and hybrid groups are very similar. There are, however, a few specific characteristics. *C. cathayensis* and *C. speciosa* appear dull dark green, while *C. japonica* is a shiny yellow-green. The leaves of *C. japonica* and of *C. cathayensis* are glabrous, while *C. speciosa* shows a few trichomes on the midribs of the under surface. The leaves of *C. cathayensis* are more finely and sharply serrate, a characteristic also evident on the young stipules which are more leaf-like on the first few leaves and become reniform on later leaves.

Seedlings of the three species of *Chaenomeles* often show such abnormalities as lobed leaves, cotyledons colored with anthocyanins, or albino leaves. Relatively often, when still in the fruit, seeds rupture and the testa and the cotyledons start to swell, and these seeds continue to grow without requiring a cold period. The seedlings obtained do not show juvenile leaves, but form a rosette of mature looking leaves. However, they do not elongate further without being submitted to a cold period.

Influence of the environment. The genus *Chaenomeles*, as shown by its morphology, is extremely plastic. Nearly all organs may present abnormalities, and some of them are so common that they can scarcely be

called aberrations. The plant may be a shrub, or, excluding *C. japonica*, be trained as a small tree. The shoots are of three types, short and long shoots on the crown, and sprouts at the base. The leaves vary a great deal in size, pubescence, and serration. The inflorescences may be of eight different kinds, according to the season. The flowers show all stages from a normal hermaphrodite condition to plants which are predominantly or completely male or female. Unisexual flowers appear usually in the spring and late fall, and a change in sex is possible from year to year in the same shrub. Fruits have two basic shapes, one developed from spring flowers, another on summer inflorescences.

Most of these differences can and do, in fact, appear on the same individual at different seasons. It is striking to observe two or more shrubs of the same clone react in the same manner under the same environmental conditions. For example, a change may occur at the same time in the sex of the flowers, or in the type of inflorescences on adjacent plants. A similar reaction to the climate is not limited to plants belonging to the same clone or even to the same species. Independent of their parental species or hybrid groups, all cultivars from Avery Island, Louisiana, are more spiny than is usual in the genus. In the specimens from Washington, D. C., the leaves are always smaller than on identical cultivars grown in other localities. Fruits are larger when coming from Georgia, but they show abnormally corky and prominent lenticels when grown in the Netherlands. Shrubs in England, usually in late spring, bear the type of inflorescence intermediate between a short and a long shoot. This type is rare elsewhere. These examples show that the genetic make-up of *Chaenomeles* allows the genus a large range of possible responses to the climate, and in part accounts for the selection of cultivars as ornamental plants on six continents.

CYTOGENETICS

Morphological and taxonomic studies show that the genus *Chaenomeles* comprises three species, namely *C. japonica*, *C. speciosa*, and *C. cathayensis*. These three species cross with each other in every possible way, forming three interspecific bihybrid groups: *C.* × *superba* (*C. japonica* × *speciosa*), *C.* × *clarkiana* (*C. cathayensis* × *japonica*), and *C.* × *vilmoriniana* (*C. cathayensis* × *speciosa*). A fourth interspecific hybrid, *C.* × *californica* (*C. cathayensis* × *superba*) is a synthesis of the three species.

Due largely to confusion of nomenclature but also to the lack of herbarium vouchers, little of the published cytogenetic information on *Chaenomeles* is reliable. Available information, however, does suggest the following:

1. The breeding behavior of *Chaenomeles* is comparable to that of its close relatives in the Maloideae, *Pyrus*, *Malus*, and *Cydonia*.

2. Hybrids within *Chaenomeles* are formed naturally under cultivation and are easily produced by artificial cross-pollination. As variations can be propa-

gated asexually these have been maintained in cultivation for long periods of time.

3. Although polyploids have been suspected, no chromosome counts support this assumption.

There was need, therefore, to repeat the previous work for confirmation; to make additional observations in an attempt to understand or explain the multitude of cultivars described for *Chaenomeles*; and to determine the relationships of *Chaenomeles* to its related taxa.

Chromosome Studies. The basic chromosome number of $x = 17$, common to all the Maloideae, was reported by Moffett (1931) for the three species of *Chaenomeles* which have $2n = 34$. He found the chromosomes of this genus to have the same morphology as those in the other genera of the Maloideae. They are small, measuring between one to three micra and, according to Moffett, possess median and submedian constrictions. Moffett's figures of meiosis in *Chaenomeles japonica* (as *Cydonia maulei*) and *C. cathayensis* show secondary pairing of the chromosomes into sexivalents, quadrivalents and bivalents. Sax (1932) thought that the apparent polyvalents might be due to Moffett's technique of sectioning, for they do not appear in smears where, at anaphase, 17 pairs pass to each pole.

In attempting to verify Moffett's work, it was found that meiosis occurs over a period of a few days, usually at the beginning of April, when the buds are 2–3 mm. in diameter on plants grown out of doors, but there is some variation due to the temperature and the cultivar used. Forced flowers proved unsatisfactory for often the stamens fail to develop properly or dry out. The young flower buds were fixed in a solution of one part glacial acetic acid and three parts 95% ethyl alcohol, and kept in the refrigerator until used. To separate the pollen mother cells, the dissected anthers were put into HCl 1 Normal for ten minutes; deposited on a slide and dried; then squashed and mounted in a drop of aceto-orcein and heated slightly. Aceto-carmine was not a satisfactory stain. Because of the small size, the chromosomes were hard to see even in good stamens at the right stage. The preparation had to be examined with the immersion objective. The pollen cells also contained oil droplets about the same size and shape and easily confused with the chromosomes.

All the species and cultivars examined were orthoploid, as in the other Maloideae, which means that they all have the same basic number. Aneuploid series have not been observed in this subfamily. The number of $x = 17$, and $2n = 34$ was confirmed in all the species. It was possible to make counts in seventeen cultivars. As diploid with $n = 17$ were: *C. japonica* 'Pigmani'; *C. speciosa* 'Contorta', 'Nivalis', 'Simonii' and 'Umbilicata'; *C.* × *superba* 'Cameo', 'Corallina', 'Glowing-Ember', 'Mount Shasta', 'Red Chief', 'Roxana Foster', 'Rowallane', and 'Texas Scarlet'; *C.* × *californica* 'California', 'Flamingo' and 'Rosy Morn'. Only one tetraploid with $n = 34$ was found, *C.* × *californica* 'Clarke's Giant Red', which has the largest flowers of all cultivars.

DOCUMENTATION OF CHROMOSOME COUNTS IN CHAENOMELES

Diploid cultivars with $n = 17$.

C. JAPONICA
  'Pigmani', Arnold Arb. No. 498–59, Weston, Mass., *Weber*, May 11, 1962 (AAH).

C. SPECIOSA
  'Contorta', Arnold Arb. No. 126–42, Jamaica Plain, Mass., *Weber*, May 6 & May 23, 1960 (AAH).
  'Nivalis', Arnold Arb. No. 13022, Jamaica Plain, Mass., *Weber*, May 6 & May 23, 1960 (AAH).
  "Simonii", Arnold Arb. No. 178–40, Jamaica Plain, Mass., *Weber*, May 6 & May 23, 1960 (AAH).
  'Umbilicata', Arnold Arb. No. 865–53, Weston, Mass., *Weber*, May 17, 1961 (AAH).

C. × SUPERBA
  'Cameo', Arnold Arb. No. 179–58, Weston, Mass., *Weber*, May 31, 1961 (AAH).
  'Corallina', Arnold Arb. No. 198–42, Jamaica Plain, Mass., *Weber*, May 6, 1960 (AAH).
  'Glowing-Ember', Arnold Arb. No. 766–57, Jamaica Plain, Mass., *Weber*, May 14, 1961 & May 9, 1962 (AAH).
  'Mount Shasta', Arnold Arb. No. 176–58, Weston, Mass., *Weber*, May 13, 1961 (AAH).
  'Red Chief', Arnold Arb. No. 486–58, Weston, Mass., *Weber*, May 17, 1961 (AAH).
  'Rowallane', Arnold Arb. No. 156–52, Weston, Mass., *Weber*, May 9, 1962 (AAH).
  'Roxana Foster', Arnold Arb. No. 483–58, Weston, Mass., *Weber*, May 9, 1962 (AAH).
  'Texas Scarlet', Arnold Arb. No. 488–58, Weston, Mass., *Weber*, May 14, 1961 (AAH).

C. × CALIFORNICA
  'California', Arnold Arb. No. 176–39, Jamaica Plain, Mass., *Weber*, May 6, 1960 (AAH).
  'Flamingo', Arnold Arb. No. 512–55, Weston, Mass., *Weber*, May 25, 1960 & May 10, 1962 (AAH).
  'Rosy Morn', Arnold Arb. No. 181–58, Weston, Mass., *Weber*, May 31, 1961 (AAH).

Tetraploid cultivar with $n = 34$.

C. × CALIFORNICA
  'Clarke's Giant Red', Arnold Arb. No. 751–60, Weston, Mass., *Weber*, May 31, 1961 (AAH).

The only known tetraploid is usually sterile, as are a few other cultivars. Occasionally, it produces fruits containing viable seeds. Since the species of *Chaenomeles* have been shown to be self incompatible, and the shrubs of 'Clarke's Giant Red' were surrounded by cultivars known to be diploid, a few seedlings were grown from one such fruit. As root tip smears are not

dependable, it is necessary to wait for the flower to determine a possible triploid condition.

Cytological investigations do not seem promising in the genus *Chaenomeles*. The pairing cannot be studied well in the genus because of the small size of the chromosomes. Meiosis was found to be normal in the species and in the hybrids, 17 chromosomes passing to each pole at anaphase. This was suspected, as the fertility appears to be normal in hybrids.

Breeding Behavior. Flowers of *Chaenomeles* are formed very early in the fall, and open in the spring before the leaves develop, or when the buds are starting to expand. The regular flowers are cup-shaped or flat, and form an easy landing platform for insects. The stigmata seem to be receptive at once and the flowers are proterogynous. The disc is nectariferous although this is not evident out of doors for the flowers are eagerly visited by ants, and nearly all of them are inhabited by thrips which must consume the nectar as soon as it is produced. Nevertheless, if flowers are kept in the refrigerator for a few days in a closed jar, nectar appears as droplets on the disc. Its taste is sweet and its peculiar odor resembles that of apples, or of maple sap. Otherwise, the flowers have no scent. The young unfolding leaves also produce liquid through the glands at about the same time. The stamens in two rows are incurved in the buds. The stamens of the outer row have straightened up by anthesis and are ready to shed pollen after a few hours or within one or two days after the flowers open. The inner row of stamens will, in turn, straighten and start to shed pollen one or more days after the stamens of the outer row. At this time, flowers are visited by honey bees, and occasionally by bumble bees. Japanese Quinces are listed by some nurseries as melliferous plants. If the weather is hot and sunny, the flowers may drop the still turgid petals while the outer row of stamens is shedding pollen. By the end of anthesis, anther sacs have tipped over and stamens become slightly versatile. When empty they change from yellow to brown.

In the spring, each flower lasts about a week, but the blooming period is longer, for flowers start to open close to the ground (which warms up earlier) and follow later along the higher branches. In spring inflorescences containing several flowers, the one in the center usually opens first, gradually followed by the others. The terminal flower is the youngest in the racemes or panicles formed in the summer, and usually is the last one to open.

When ripe, the fruits do not persist long on the shrubs. They often drop all at once, probably due to frost. When the fruits are on the ground (but sometimes while still on the shrubs) they are opened by birds seeking the seeds. The flesh is very acid and does not seem to be eaten. The seeds are also eagerly collected by rodents. A burrow (of rats?) was observed under a shrub of Japanese Quince and split open fruits were carefully piled up as refuse on both sides of the entrance. No seeds were left on the rejected cores, but were probably stored underground.

Most likely, the seeds of *Chaenomeles* are dispersed by birds and small animals, when gathering food for winter preserves. A shrub, as a garden escape, was observed by Fernald in a hedge at Barnstable, Mass. Japanese Quinces are also known to become naturalized in Japan and Korea. In cultivation, no seedlings have been observed close to mature shrubs. This may be due to the numerous animals eating the seeds. Flocks of pigeons have been observed repeatedly near Japanese Quinces when the fruits were on the ground. It is difficult to believe that large seeds, often already breaking the seed coat inside the fruits, can pass undigested through the intestinal tract of a bird, but enough must be lost by the animals collecting the seeds to ensure reproduction in the wild.

From old observations, *Chaenomeles* was suspected to be self incompatible but the possibility of apomixis had to be investigated since it is of frequent occurrence in *Malus* and other genera of the Maloideae. It is recorded that *C. speciosa*, when introduced into Europe at the end of the eighteenth century, did not bear fruits for many years. At that time, it was believed that the temperature was not adequate for fruit production. Shrubs often were kept in greenhouses but still did not form fruit. When Japanese Quinces became common, and many varieties were grown in adjacent areas, fruits appeared in any climate. The early reports of no fruit development were certainly due to self incompatibility as subsequent experiments seem to have demonstrated.

Apomixis includes reproduction in which embryos (and seeds) are produced asexually (agamospermy). Simple experiments involving the bagging of flowers or the isolation of plants may give the first indication of the presence or absence of this phenomenon. Colby (1929) bagged various cultivars of *Chaenomeles* and reported that except for *C. speciosa* 'Grandiflora', no fruits were produced. Similar experiments were performed for this study on *C. speciosa* 'Early Apple Blossom'; *C.* × *superba* 'Columbia', 'Sunset', and 'Superba'; as well as on *C.* × *californica* 'California'. No fruits were produced. The explanation of fruit production in one cultivar is not clear. The flowers of *Chaenomeles* are visited by ants and extremely small insects attracted by the nectar present inside the floral cup at anthesis and along the unfolding leaves. It is possible that these small insects penetrated the bag placed around a branch of *C. speciosa* 'Grandiflora'. A word of caution must be expressed. The position of the flower clusters of *Chaenomeles* on old wood, requires the shoot system to be enclosed in plastic or paper bags. Artificial conditions of heat and moisture are evident in the bag and are detrimental to the young foliage and perhaps to the flowers. However, in most cases sufficient normal shoot development was observed to eliminate this factor in accounting for the lack of fruit production.

A second test of apomixis and self incompatibility was made by the observation of isolated plants without bagging, and insect pollination limited to natural selfing. A shrub of *C. speciosa* located near the Harvard Law School was observed for two years during which it did not produce fruits. The closest Japanese Quinces, members of the Superba group,

are in the Cambridge Common, a distance of about 200 meters. In the spring of 1962, flowers of *C.* × *superba* were used to pollinate, by hand, a few flowers of the isolated specimen of *C. speciosa* at the Law School. The artificially pollinated flowers were tagged and all of them produced fruits. No fruits were formed from flowers not cross pollinated by hand. The seeds were sown, and all the seedlings showed traces of hybridization between *C. speciosa* and *C.* × *superba*. In another experiment, to serve as a control, a shrub of *C.* × *superba* 'Knap Hill Scarlet' known for its fruit production was transplanted from the shrub collection of the Arnold Arboretum in Jamaica Plain to an isolated spot in Cambridge. It bloomed abundantly in its new location during the spring of 1962, but in spite of numerous bees that visited the flowers, not one fruit was formed.

The same condition occurred in a plant of *C. speciosa* 'Tani-no-Yuki' and one of *C.* × *superba* 'Otto Froebel' moved into the greenhouse. In the absence of pollinators to effect cross pollination, no fruits were produced. A few flowers were self-pollinated by hand and these also failed to develop fruits. However, a few flowers were cross-pollinated between the two varieties and all produced fruits with fully developed ovules. In addition to the fruit formation, the pistils of these self- and cross-pollinated flowers were also observed. The styles were collected from one to three days after hand pollination; dipped for two days in Gentian violet and then mounted in lactophenol. Under a microscope, it was possible to examine the growth of the pollen tubes.

Self-pollinated flowers of *Chaenomeles* have been observed to have aberrant pollen development. When pollen is placed on the stigmata there may be complete failure of pollen tube development or the tube may develop and not penetrate the stigmatoid or stylar tissues. In such flowers there may be a slight swelling of the hypanthium but the resulting small fruits turn yellow and fall within a few weeks. Sections of such fruits show no ovule development.

In the collections of the Arnold Arboretum many cultivars of *Chaenomeles* are grown side by side in rows. With this abundance of plants fruit production is usually heavy, although some cultivars remains sterile year after year. In contrast, in the Boston suburbs isolated plants may be found as ornamental shrubs in gardens, which rarely fruit or produce malformed fruits containing a reduced number of seeds, but never less than four. There seems to be no parthenocarpy as in *Malus*, where fruits of normal appearance may be formed without seeds.

Hall (1931) studied the problem of fruit failure in the apple and recorded that the fruit production of a given variety may be inconsistent. A variety which is self sterile under one set of conditions may be self fertile under another. Self incompatibility may be the result of genetic factors but environmental factors may also influence fruit production.

Hybrids. Intergeneric hybrids are of common occurrence in the Maloideae, but none are recorded with *Chaenomeles* as one of the parents in spite of the common chromosome number $2n = 34$, and the same

chromosome morphology. Crosses between the two species of *Cydonia* and species of *Chaenomeles* were unsuccessful in several attempts. Crosses with other genera should be tried. The three species of *Chaenomeles* have been shown to be completely interfertile under cultivation and there seems to be no reduction of fertility in subsequent generations of hybrids. This should, however, be tested statistically. Genetically, *Chaenomeles* appears to be a distinct taxon.

Self incompatibility in ornamental plants favors the production of hybrids by natural and artificial means. There was very little variation in *Chaenomeles* during the first twenty years after the introduction of *C. speciosa* from Japan into Europe, in 1796. During this period, all plants were probably propagated asexually from the first shrub introduced at Kew Gardens, as no fruits were produced. One variety with blush flowers, called white, existed very early, and may have been a separate introduction. It was only after 1830 when von Siebold returned from Japan with many color forms of *C. speciosa* that varieties were developed in Japanese Quinces by the selection of seedlings. The colored forms, grown side by side, certainly crossed naturally. Before the introduction of any other species, numerous selections had been made in *C. speciosa* on the basis of variation in flower color, in number of petals, in the shape of the fruits, and in the size of the plants. The selections made over a century ago were the start of clonal lines which, through asexual propagation, are still grown in many gardens.

In 1869, a second species, *C. japonica*, was introduced into Europe. This species was distributed to gardens where *C. speciosa* was planted, and from the beginning set fruits. *C. japonica* was reproduced by seeds, and was thought to breed true. Very soon, numerous color forms appeared in the progeny of this species. They were considered varieties, but later all proved to be natural hybrids with *C. speciosa*. Such was the origin of *C. × superba*. In recent years, numerous cultivars have been added to this group by selection, or by deliberate crossing of the two parental species.

C. cathayensis, introduced into Europe around 1880, appears to be very uniform, but more observations must be made on this species before its breeding behavior can be ascertained. This species is closest to *Cydonia* which contains two species known to be self compatible. The hybrid groups *C. × clarkiana*, *C. × vilmoriniana*, and *C. × californica* were produced by hand pollinating flowers of two different species, or, the latter by pollinating flowers of an interspecific hybrid by a third species. The progeny of the interspecific hybrids proved to be fertile with other hybrids, or with any of the parents. As a result, *Chaenomeles* has an amount of variation unequalled in the other genera of the Maloideae partially due to backcrossing and introgression.

The taxonomic treatment of several hundred cultivars of *Chaenomeles* presents a significant problem. The horticulturist would accept a grouping based on the color of the flower, the form of the flower, single, semi-double or double, or perhaps a classification based on hardiness, fruit

shape, or habit. The botanical approach requires recognition of the
parent species and suggests that the cultivars be treated as a hybrid
swarm. The fundamental information on the species was obtained by a
study of herbarium specimens collected in the localities where the species
are not found together. *C. japonica* is restricted to Japan where no other
species is native. *C. speciosa* and *C. cathayensis* are from China. The
sparse collections and the lack of data on their distribution and ecology
do not indicate whether they grow together within their sympatric range,
but no hybrids of these species have been recorded in China, and none
were found among the herbarium specimens. Information on individual
variation within a pure species was also available from shrubs grown
from seeds of wild plants.

The morphological variation of the species is extreme and it was, there-
fore, impractical to apply the usual techniques of scatter diagrams, ideo-
graphs or hybrid indices for this reason, and because of the numerous
cultivars of the Californica group which are hybrids of not two but three
species. A different method had to be devised to analyse each of the
more than 300 named cultivars produced by variation within three species,
by simple crosses in four combinations, and by backcrosses with subse-
quent asexual propagation. Anderson's techniques inspired the method
used in this study.

Herbarium specimens of cultivars were gathered from different localities
to observe the differences due to the environment. These specimens were
supplemented by colored drawings of fresh flowers. The drawings, more
reliable than colored photographs, allowed a comparison of characters
important to the horticulturist, but not easily preserved in dried specimens.
Since numerical evaluation could not be used with trihybrids, the usual
scoring was replaced by attributing each morphological character of the
cultivar, such as habit, twig, leaf, flower, and fruit to the species it re-
sembled most. It was found that the different organs usually tended to be
closer to the type encountered in one of the species, perhaps because of the
presence of linked genes, or at least of several genes on a single chromo-
some affecting the same organs. When the characters were intermediate,
this was indicated. From the results of the listing, each cultivar was
attributed to a species, or to a hybrid group, when possessing charac-
teristics of more than one species. The records of the parentage of crosses
made by a few nurserymen were generously supplied and in most cases
substantiated the recording technique. On several occasions cultivars,
supposedly authentic, could not have been produced by the parentage
suggested, and indicated an error in the identification of the cultivar, or
one of its parents. Many cultivars in *Chaenomeles* are known to be
backcrosses. Others suggest that introgression has advanced far in the
Japanese Quinces. As Anderson stated "In the second generation of
hybrids and in backcrosses there will be various and multitudinous re-
combinations of flower color, shapes and heights and no two plants will
look very much alike." This explains why so many cultivars can be
produced from three basic species.

The relative ease with which characteristics of habit, twig, leaf, flower, and fruit could be attributed to the parents of one species or another, permits identification of the parents of a hybrid, and also prediction as to the progeny of the cross. After the intercorrelated characters were sorted, it was possible to list those characters tending to appear together. For example, a cultivar with orange petals always has crenate leaves, warted twigs, and is of medium size. These characters come from its parent, *C. japonica*. Leaves with serrations terminated by an awn-like tip usually show some pubescence on the under surface, both characters coming from *C. cathayensis*. Having so many hybrids of known parentage, it was possible to recognize the characteristics which tend to be expressed.

The members of the Superba group, *C. japonica* × *speciosa*, usually are shrubs of intermediate size and branching. The twigs have the warting of *C. japonica*. The leaves are intermediate between the leaves of the two species, or more japonica-like as far as the color (dark green in *C. speciosa*, yellow-green in *C. japonica*), pubescence, and serration are concerned. The flowers have the wide range of color of *C. speciosa*, with the addition of pure orange found only in this group as a combination of the salmon pink of *C. japonica* with the red of the other species. Fruits are intermediate in size and perhaps in shape, but are closer to those of *C. japonica*. The sticky skin in many hybrids is also derived from *C. japonica*. The seeds, which are very similar in shape and size, may be differentiated only by the shiny testa of *C. japonica*, often present in seeds of the hybrids, versus the dull testa of *C. speciosa*.

The three cultivars of the Vilmoriniana group, *C. cathayensis* × *speciosa*, are intermediate as far as characteristics of the habit and twigs are concerned, but show the influence of *C. cathayensis* in the other characters.

These two hybrid groups show that in a cross of *C. japonica* × *speciosa*, the characters of *C. japonica* tend to be expressed over those of *C. speciosa*; in a cross of *C. cathayensis* × *speciosa* the progeny will look more like *C. cathayensis*. It is interesting to compare these observations with the characters of the cultivars of the Clarkiana group, *C. cathayensis* × *japonica*. Although two cultivars only are in this group, they are both intermediate in all their parts and neither parent dominates the other.

An analysis of the numerous cultivars of the Californica group, *C. cathayensis* × *superba* reveals mostly intermediate characters, those of *C. cathayensis* tending to be expressed in the shape and size of the shrubs, in the spines, and often in the fruits. The flowers encompass the range of color found in *C. speciosa*, but are often of two tones of pink, brighter but very much like the flowers of *C. cathayensis*.

These results, obtained from a study of the existing cultivars, may serve as a guide for the plant breeder wanting to produce a certain type of shrub. Size is certainly due to multiple genes, being in the range of the size of the parental species. Branching and spininess of *C. japonica* tend to be expressed when crossed with *C. speciosa*. In a cross including *C. cathayensis* as one parent, the shrub will look more like *C. cathayensis* than any other. The warting of *C. japonica* is always present in its pro-

geny, and is an important character in detecting hybridization with this species. *C. japonica* leaves, characterized by glabrescence and crenate teeth, may be contrasted with the leaves of *C. cathayensis*, showing serration, terminated by an awn-like tip and abundant fulvous tomentum on the under surface at maturity. The leaf characters of *C. japonica* and of *C. cathayensis* again, tend to be expressed over those of *C. speciosa*. Interspecific hybrids, including the two dominant species, possess leaves intermediate in size, serration, and pubescence between those of the parents. The flowers are usually intermediate, taking up the range of color of the species with the largest range. A new color, orange, has appeared in hybrids by combination of pigments separately present in *C. japonica* and *C. speciosa*. In hybrids including *C. cathayensis*, flowers are often bicolored as in this species. The fruits tend to be intermediate in shape and size between those of the two parents; the ovoid shape of *C. cathayensis* appearing often in its hybrids. In the seeds, the wedge-shape of *C. cathayensis* is expressed over the unspecified shape of *C. speciosa* (found also in *C. japonica*), while seed characteristics of *C. japonica* dominate those of the others in shape, size, and the nature of the testa. To these morphological characters may be added the physiological one of hardiness. In a cross between a hardy species and one which is not, the lack of hardiness, probably due to multiple genes (as present in *C. cathayensis*) is usually expressed.

This survey of the morphological characters and behavior of the different cultivars belonging to the three species, and to the four hybrid groups shows that *C. cathayensis* and *C. japonica* are two well defined species. Their morphological characters are easily recognized, and are evident in their progeny. This is not the case with *C. speciosa*, which is less specialized and does not possess characters not present in some degree in the other two species. This was evident when preparing the key to distinguish species and hybrid groups. The separation was found to be difficult between the cultivars belonging to *C. speciosa* and those of *C.* × *clarkiana*, a hybrid between *C. cathayensis* and *C. japonica*.

Evreinoff (1937) quotes Pachkevitch (1930) as saying that he believed *C. lagenaria* to be a hybrid between the other two species. The nomenclature is so confused in Evreinoff's paper that it is not possible to ascertain whether *C. lagenaria* in his sense means *C. speciosa* or *C. cathayensis*. Unfortunately, Pachkevitch's treatise on pomology, in Russian, could not be obtained. His idea of the origin of one of the species of *Chaenomeles* by hybridization of the other two is appealing. It would explain why *C. speciosa* has no morphological character and range of its own, and why it is by far the most variable species in cultivation as well as in a native state. It may also suggest an explanation of the fact that the three species are still so closely related that they cross freely when grown in gardens. *C. japonica* is native only in Japan, *C. cathayensis* and *C. speciosa* probably occurring in different habitats in the region of Yunnan, China, did not develop reproductive isolation because other isolation mechanisms are present to keep them apart in the wild.

[*To be concluded*]