FLORAL ONTOGENY AND MORPHOLOGY IN SUBFAMILY SPIRAEOIDEAE ENDL. (ROSACEAE)

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“Spiraeoideae,” as traditionally circumscribed, contain the greatest diversity of floral organ morphology of any of the four subfamilies in the Rosaceae. Comparisons of mature floral morphology in 10 spiraeoid genera demonstrate that genera in this subfamily exhibit many floral character states present in the other three subfamilies. Inflorescence development, gynoecium initiation and development, ovule development and morphology, and obturator position all exhibit considerable variation in these taxa. Inflorescences vary from simple and racemose to multibranched and cymose. Gynoecial appendages can be initiated as independent primordia or from a shallow gynoecial ring primordium. Placenta occurs on the ventral margin of the ovary locule and includes apotropic ovules inserted near the base (Porteranthus and Vauqueлина), apotropic and pleurotropic ovules inserted the entire length or midway (Kagenekia and Physocarpus), and apically inserted epipetalous ovules (Anunnus, Chamaebatiaria, Holodiscus, Lyonothamnus, Sorbaria, and Spiraea). Associated with the ovules of almost all genera is an obturator that may comprise cells of the funiculus or cells of both the funiculus and locule margin. These results corroborate those of other studies that suggest that the “Spiraeoideae” are an artificial, polyphyletic group.

Keywords: systematics, phylogeny, inflorescence typology, gynoecium, ovules, obturators.

Introduction

The “Spiraeoideae” includes approximately 20 small genera scattered from South America north into Central and North America and Eurasia. Traditionally circumscribed as a subfamily (e.g., Rehder 1940; Thorne 1983), some classifications advocate a tribal classification for these genera (table 1; Hutchinson 1964; Schulze-Menz 1964) as well as for all of the Rosoideae (Hutchinson 1964; Schulze-Menz 1964). Results of recent studies (Morgan et al. 1994; Takhtajan 1997), however, demonstrate that the “Spiraeoideae” are a polyphyletic group that does not correspond to tribal circumscriptions.

Comparative analyses of mature morphology (Sterling 1966b; Schaeppi and Frank 1967; Kalkman 1988) and phylogenetic analyses of wood anatomy (Zhang 1992) and DNA sequence variation (rbcL, Morgan et al. 1994; nrITS, Campbell et al. 1995) provide a variety of results concerning relationships within the “Spiraeoideae,” as well as their relationships to the rest of the Rosaceae. Kalkman (1988) separated the “Spiraeoideae” into seven “operational units,” and his cladistic analysis of 14 morphological characters resulted in a clade that was basal to the rest of the Rosaceae (Kalkman 1988, fig. 1), unresolved, but for the most part represented a monophyletic “Spiraeoideae.” Schaeppi and Frank (1967) studied receptacle and carpel morphology in seven spiraeoid genera and concluded that they form a natural group that demonstrates primitive floral character states, share a close association to subfamilies Maloideae and Prunoideae, and are similar in carpel morphology to the Crassulaceae. Sterling (1966b) and Challiche (1974, 1981), although not commenting on outgroup relationships, also hypothesized a spiraeoid-like ancestor to the Rosaceae on the basis of floral vasculature and ovary closure, and chemotaxonomy, respectively.

Zhang (1992) used 18 wood anatomy characters, chromosome number, and fruit (in-)dehiscence to infer relationships for 62 rosaceous genera from the four subfamilies. Zhang’s results, although demonstrating the polyphyly of the “Spiraeoideae,” a paraphyletic tribe Quillajeae, and relationships between spiraeoid genera and members of the Rosoideae, should be considered tentative because his analyses are incomplete and the positions of some genera “are a consequence of very minor wood anatomical differences, sometimes in features of limited diagnostic value” (Zhang 1992, p. 109). Results from rbcL sequence analyses (Morgan et al. 1994) are similar to Zhang’s with respect to the polyphyly of the “Spiraeoideae,” and the close relationship of some spiraeoid genera with those of the Rosoideae. Tribe Quillajeae, however, is polyphyletic, justifying the removal of Quillaja from the Rosaceae entirely, the inclusion of Exochorda in Amygdaloideae sensu lato, the placement of Lyonothamnus as sister to Cercocarpus and Parshia (two rosoid genera), and the placement of Kagenekia, Lindleyea, and Vauquelinia as basal in the Maloideae (Morgan et al. 1994). Further justification for the placement of Vauquelinia in the Maloideae is demonstrated by analyses of nuclear DNA sequence variation (nrITS, Campbell et al. 1995). Although these three genera are traditionally placed in the “Spiraeoideae” because of their follicular (Kagenekia) or capsular (Lindleyea and Vauquelinia) fruits, analyses of chromo-
Table 1

Comparison of Different Treatments of Subfamily “Spiraeoideae”

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<tr>
<td>Aruncus Adans. ..................</td>
<td>Bentham and Hooker 1862-1867</td>
<td>...</td>
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<td>...</td>
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<td>...</td>
</tr>
<tr>
<td>Chamaebataria Maxim. ..........</td>
<td>Bentham and Hooker 1862-1867</td>
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<td>...</td>
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<td>...</td>
<td>...</td>
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<tr>
<td>Exochorda Lindl. ................</td>
<td>Bentham and Hooker 1862-1867</td>
<td>...</td>
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<tr>
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<td>Bentham and Hooker 1862-1867</td>
<td>...</td>
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</tr>
<tr>
<td>Lyonothamnus A. Gray .............</td>
<td>Bentham and Hooker 1862-1867</td>
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<td>...</td>
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<tr>
<td>Kageneckia Ruiz &amp; Pav. .........</td>
<td>Bentham and Hooker 1862-1867</td>
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<td>...</td>
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<td>Physocarpus Maxim. ...............</td>
<td>Bentham and Hooker 1862-1867</td>
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<td>Porteranthus Britton ............</td>
<td>Bentham and Hooker 1862-1867</td>
<td>...</td>
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<td>...</td>
<td>...</td>
</tr>
<tr>
<td>Sorbaria A. Braun ...............</td>
<td>Bentham and Hooker 1862-1867</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>...</td>
</tr>
<tr>
<td>Vauquelinia Correa ex Humb. &amp; Bonpl.</td>
<td>Bentham and Hooker 1862-1867</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>...</td>
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</tbody>
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* Genus not yet described.
* Previously studied (Evans and Dickinson 1999).

some number and floral characters agree with the placement of at least Vauquelinia and Lindleya within the Maloideae (Stebbins 1958; Sterling 1966b; Goldblatt 1976; Hess and Henrickson 1987).

In another article (Evans and Dickinson 1999, in this issue), we confirmed, through comparisons of floral ontogeny and morphology, that Exochorda belongs in subfamily Amygdaloideae s.l., as has been suggested earlier (Goldblatt 1976; Dahlgren 1983; Thorne 1983; Zhang 1992; Morgan et al. 1994; Takhtajan 1997). Our goal here is to examine the variation in mature morphology displayed by spiraeoid taxa and to test relationships suggested by recent phylogenetic analyses (Kalkman 1988; Zhang 1992; Morgan et al. 1994). To determine the developmental basis for differences in floral morphology, we examined four taxa—Physocarpus, Sorbaria, Spiraea, and Vauquelinia— that represent the range of variation displayed by “Spiraeoideae.” Specifically, we seek to answer the following questions: (1) Do the ontogeny and morphology of spiraeoid flowers provide additional evidence for recent phylogenetic hypotheses of spiraeoid relationships? and (2) Can ontogenetic and morphological data aid in the evaluation of hypotheses concerning the origin of the Maloideae, whether from “Spiraeoideae” alone (Gladkova 1972; Cronquist 1981; Morgan et al. 1994; Takhtajan 1997) or paleohybridization between “Spiraeoideae” and Amygdaloideae (Sax 1933; Stebbins 1950, 1958; Challice 1974, 1981; Phipps et al. 1991; Rohrer et al. 1991; Morgan et al. 1994)?

Material and Methods

Plant material for ontogenetic studies was collected from garden and wild accessions (table 2). At least 15 inflorescences or mature flowers from each collection were dissected and processed for microscopic analysis. Techniques and equipment used in preparing samples, scanning electron microscopy (SEM), embedding in plastic and paraffin, sectioning, and staining have been described elsewhere (Evans and Dickinson 1999, in this issue).

Results

Mature Morphology

Inflorescences of taxa in this study comprise corymbs (Kageneckia, Spiraea trilobata, and Physocarpus), compound cor-
### Table 2

<table>
<thead>
<tr>
<th>Taxa studied</th>
<th>Garden accession no. or herbarium voucher</th>
<th>Collection site</th>
<th>Collection dates</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Chamaebatiaria millefolium</em> (Torr.) Maxim. .................</td>
<td>...</td>
<td>Along forest service road in Inyo National Forest on White Mtns., 3.5 mi N of Schulman Grove, California</td>
<td>August 20, 1997</td>
</tr>
<tr>
<td><em>Holodiscus discolor</em> (Pursh) Maxim. ......</td>
<td>13589</td>
<td>Rancho Santa Anna Botanical Garden, California</td>
<td>April 23, 1997</td>
</tr>
<tr>
<td><em>Kageneckia angustifolia</em> D. Don ..........</td>
<td>80.0176</td>
<td>University of California, Berkeley, Botanical Garden</td>
<td>April 25, 1997</td>
</tr>
<tr>
<td><em>Lyonothenus floribundus</em> var. <em>asplenifolius</em> A. Gray .................</td>
<td>UD6464</td>
<td>Rancho Santa Anna Botanical Garden, California</td>
<td>April 23, 1997</td>
</tr>
<tr>
<td><em>L. floribundus</em> var. <em>asplenifolius</em> ..........</td>
<td>80.0098</td>
<td>University of California, Berkeley, Botanical Garden</td>
<td>June 5, 1997</td>
</tr>
<tr>
<td><em>Physocarpus bracteatus</em> (Rydb.) Rehd. .................</td>
<td>1235-85</td>
<td>Arnold Arboretum</td>
<td>June 13, 1996</td>
</tr>
<tr>
<td><em>Physocarpus opulifolius</em> (L.) Maxim.&lt;sup&gt;b&lt;/sup&gt; ....................</td>
<td>800909</td>
<td>Royal Botanical Gardens, Hamilton</td>
<td>March 31–June 26, 1995 (weekly)</td>
</tr>
<tr>
<td><em>P. opulifolius</em> var. “Luteus”&lt;sup&gt;ab&lt;/sup&gt; .................</td>
<td>XX256</td>
<td>Royal Botanical Gardens, Hamilton</td>
<td>March 31–June 26, 1995 (weekly)</td>
</tr>
<tr>
<td><em>Porteranthus trifoliatus</em> Britton (=<em>Gillenia trifoliata</em> [L.]) Moench) .................</td>
<td>Evans 466 (TRT)&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Blue Ridge Pkwy., 3 mi N of Minerals Museum, North Carolina</td>
<td>June 18, 1997</td>
</tr>
<tr>
<td><em>Sorbaria sorbifolia</em> (L.) A. Br.&lt;sup&gt;c&lt;/sup&gt; ..........</td>
<td>871064</td>
<td>Royal Botanical Gardens, Hamilton</td>
<td>March 31–July 21, 1995 (weekly)</td>
</tr>
<tr>
<td><em>Spiraea alba</em> Du Roi .........................</td>
<td>800205</td>
<td>Royal Botanical Gardens, Hamilton</td>
<td>July 21, 1995</td>
</tr>
<tr>
<td><em>Spiraea trifoliate</em> L.&lt;sup&gt;c&lt;/sup&gt; ....................</td>
<td>Evans 457 (TRT)&lt;sup&gt;a&lt;/sup&gt;</td>
<td>University of Toronto campus</td>
<td>April 3–June 4, 1997 (weekly)</td>
</tr>
<tr>
<td><em>Vauquelinia californica</em> (Torr.) Sarg&lt;sup&gt;b&lt;/sup&gt; ...............</td>
<td>Evans 419, Dickinson 1719–1721 (TRT)&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Molino Basin Picnic Area, Arizona</td>
<td>April 22, 1997; June 2, 1998</td>
</tr>
<tr>
<td><em>V. californica</em>&lt;sup&gt;c&lt;/sup&gt; .........................</td>
<td>40.114</td>
<td>Boyce Thompson Southwest Arboretum, Arizona</td>
<td>April 22, 1997; June 3, 1998</td>
</tr>
</tbody>
</table>

<sup>a</sup> Vascular Plant Herbarium, Royal Ontario Museum.
<sup>b</sup> Taxa used in ontogenetic studies.

Ymb (Vauquelinia), panicles (Chamaebatiaria, Holodiscus, Spiraea alba, Sorbaria sorbifolia, Aruncus, and Porteranthus), and cymes (Lyonothenus) are evergreen and flower in late spring to early summer. Appearance of inflorescences in the deciduous taxa occurs after the appearance of short shoot leaves in late spring (Holodiscus), midsummer (Aruncus, Physocarpus, Spiraea, and Porteranthus), or late summer (Chamaebatiaria and Sorbaria). Inflorescences of all taxa terminate short shoots that are axillary on long shoots from the previous season or terminate a
TABLE 3

Morphological Variation in Some Taxa of Subfamily “Spiraeoideae”

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Inflorescence morphology</th>
<th>Sepal no.</th>
<th>Petal no.</th>
<th>Stamen no.</th>
<th>Pistil no.</th>
<th>Ovary suture closure</th>
<th>Ovule no.</th>
<th>Ovule morphology</th>
<th>Integument no./continuity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aruncus dioicus</td>
<td>Panicle of compound racemes</td>
<td>5</td>
<td>5</td>
<td>20</td>
<td>3–4</td>
<td>Appressed</td>
<td>6–8</td>
<td>Apical epitropic</td>
<td>1</td>
</tr>
<tr>
<td>Chamaebatiaria millefolium</td>
<td>Panicle</td>
<td>5</td>
<td>5</td>
<td>60</td>
<td>5</td>
<td>Appressed</td>
<td>6–8</td>
<td>Apical epitropic</td>
<td>2/continuous</td>
</tr>
<tr>
<td>Holodiscus discolor</td>
<td>Panicle</td>
<td>5</td>
<td>5</td>
<td>20</td>
<td>5</td>
<td>Fused</td>
<td>2</td>
<td>Apical epitropic</td>
<td>1</td>
</tr>
<tr>
<td>Kageneckia oblonga</td>
<td>Single flower/raceme</td>
<td>5</td>
<td>5</td>
<td>15–20</td>
<td>5</td>
<td>Appressed</td>
<td>14–20</td>
<td>Pleurotropic files</td>
<td>1</td>
</tr>
<tr>
<td>Kageneckia angustifolia</td>
<td>Single flower/raceme</td>
<td>5</td>
<td>5</td>
<td>20</td>
<td>5</td>
<td>Appressed</td>
<td>14–20</td>
<td>Pleurotropic files</td>
<td>2/continuous</td>
</tr>
<tr>
<td>Lyonothamnus floribundus var. asplenifolius</td>
<td>Cyme</td>
<td>5</td>
<td>5</td>
<td>20</td>
<td>2</td>
<td>Appressed</td>
<td>4–6</td>
<td>Apical epitropic</td>
<td>2/free</td>
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<tr>
<td>Physocarpus bracteatus</td>
<td>Corymb</td>
<td>5</td>
<td>5</td>
<td>20</td>
<td>3</td>
<td>Appressed</td>
<td>2–4</td>
<td>Mid pleurotropic mid apotrophic</td>
<td>2/continuous</td>
</tr>
<tr>
<td>Physocarpus opulifolius</td>
<td>Corymb</td>
<td>5</td>
<td>5</td>
<td>20</td>
<td>(3–)5</td>
<td>Appressed</td>
<td>2–4</td>
<td>Mid pleurotropic mid apotrophic</td>
<td>2/continuous</td>
</tr>
<tr>
<td>P. opulifolius “Luteus”</td>
<td>Corymb</td>
<td>5</td>
<td>5</td>
<td>20</td>
<td>(3–)5</td>
<td>Appressed</td>
<td>2–4</td>
<td>Mid pleurotropic mid apotrophic</td>
<td>2/continuous</td>
</tr>
<tr>
<td>Porteranthus trifoliatus</td>
<td>Panicle</td>
<td>5</td>
<td>5</td>
<td>20</td>
<td>5</td>
<td>Appressed</td>
<td>2</td>
<td>Basal apotrophic Apical epitropic</td>
<td>2/continuous</td>
</tr>
<tr>
<td>Sorbaria sorbifolia</td>
<td>Panicle</td>
<td>5</td>
<td>5</td>
<td>25–30</td>
<td>5</td>
<td>Appressed</td>
<td>6–8</td>
<td>Apical epitropic Basal apotrophic</td>
<td>2/continuous</td>
</tr>
<tr>
<td>Spiraea alba</td>
<td>Panicle</td>
<td>5</td>
<td>5</td>
<td>20</td>
<td>5</td>
<td>Appressed</td>
<td>6–8</td>
<td>Apical epitropic Basal apotrophic</td>
<td>1</td>
</tr>
<tr>
<td>Spiraea trilobata</td>
<td>Corymb</td>
<td>5</td>
<td>5</td>
<td>20</td>
<td>5</td>
<td>Appressed</td>
<td>6–8</td>
<td>Apical epitropic Basal apotrophic</td>
<td>1</td>
</tr>
<tr>
<td>Vauquelinia californica</td>
<td>Compound corymb</td>
<td>5</td>
<td>5</td>
<td>20</td>
<td>5</td>
<td>Appressed</td>
<td>2</td>
<td>Basal apotrophic Basal apotrophic</td>
<td>2/continuous</td>
</tr>
</tbody>
</table>

1. Ovary closure designated fused if postgenital fusion seals suture and cells of margin epidermis not visible where suture occurs; designated appressed if cells of margin epidermis visible in suture.
2. Ovules designated apical if inserted in upper half of locule, mid if inserted within mid portion of locule margin, basal if inserted near base of locule margin. Ovules designated epitropic if micropyle superior to chalaza, pleurotropic if micropyle parallel to floral apex (=even with chalaza), and apotrophic if micropyle inferior to chalaza.
3. Integuments considered free if spaces visible between integuments; continuous if no space visible.
4. Absent (Aruncus; fig. 2.3) or sterile (Kageneckia; not shown) in female flowers.
5. Present in male flowers, but ovules are underdeveloped at maturity (fig. 2.2).
6. Only present in female flowers.

short shoot from the previous season. Chamaebatiaria and Sorbaria differ from the other taxa in that considerable vegetative shoot development occurs before inflorescences become visible on the new shoot.

All taxa examined in this study have flowers that are typical of Rosaceae. The flowers are actinomorphic and possess a perianth that is inserted on the rim of a hypanthial cup and consists of five white petals alternating with five green sepals. All taxa studied have perfect flowers except Aruncus dioicus, Kageneckia oblonga, and Kageneckia angustifolia, which are dioecious. Nectaries are comparable in all taxa and consist of a band of stomatal-porous tissue that extends between the base of the stamens and near the base of the ovaries (Schaeppi and Frank 1967). Spiraea flowers differ slightly in nectary morphology, as their nectaries appear as small pads between the stamen filaments (Schaeppi and Frank 1967). Stamen number ranges from 15 in Kageneckia to 60 in Chamaebatiaria, with the majority of genera having 20 (table 3). The gynoecia of Chamaebatiaria, Kageneckia, Physocarpus opulifolius, Porteranthus, Sorbaria, Spiraea, and Vauquelinia are pentameroous (table 3). In contrast, Lyonothamnus, Physocarpus bracteatus, and Aruncus have two- to four-merous gynoecia (table 3). Ovary connation and adnation varies from no connation or adnation (Aruncus, Holodiscus, Kageneckia, and Spiraea), to connate only (Lyonothamnus, Physocarpus, and Porteranthus), to connate as well as basally adnate to the hypanthium (Chamaebatiaria, Sorbaria, and Vauquelinia). The ventral ovary sutures at the point of ovule insertion are closed at maturity in all taxa either by the appression of adjacent ventral margin epidermal layers (Aruncus, Chamaebatiaria, Kageneckia, Lyonothamnus, Physocarpus, Porteranthus, Sorbaria,
Variation in Ovule Number, Position in the Ovary, and Morphology

The genera examined display a great variation in ovule number, ovule position within the ovary, and integument number (table 3; Robertson 1974; Rohrer et al. 1994; Evans 1999). Ovule number varies from two to 20, and ovule insertion within the locule varies from epitropic and apical to pleurotropic, to apotropc and near the base (fig. 1). The majority of taxa (Aruncus female and male flowers, Chamaebatiaria, Lyonothamnus, Sorbaria, and Spiraea) have four to eight ovules per locule that are epitropic and inserted apically on the ventral margin (figs. 2.2–2.6, 4, 14.67, 17.83). The ovaries of female flowers of Kageneckia contain 14–20 pleurotropic ovules per locule, positioned in files along the length of the ventral ovary margin (figs. 3.9, 6.22, 6.23). Physocarpus have ovule numbers that vary from two to four per locule, and their
Fig. 2  Scanning electron micrographs of mature flowers and ovules in *Aruncus, Chamaebatiaria, and Holodiscus*. Fig. 2.2, Dissected male *Aruncus* flowers with multiple stamens (A) and aborted ovules (O). Fig. 2.3, Dissected female *Aruncus* flower lacking stamens, but ovaries contain fully developed ovules (O). Fig. 2.4, Close-up of dissected female *Aruncus* ovary showing two apically inserted, epitropic ovules (O) with obturator (Ob) composed of cells from the funiculus and ventral ovary margin. Fig. 2.5, Dissected *Chamaebatiaria* flower with multiovulate (O) ovaries. Fig. 2.6, Close-up of *Chamaebatiaria* ovary with multiple, apically inserted, epitropic ovules (O) with obturators (Ob) composed of cells from the funiculus and ventral margin wall. Fig. 2.7, Dissected *Holodiscus* flower with dissected ovary. Ne, nectary; A, stamen; O, ovule; Sg, stigma; Sy, style. Scale bars = 100 μm on figs. 2.2–2.4 and 2.6, 500 μm on figs. 2.5 and 2.7.
Fig. 3 Scanning electron micrographs of mature flowers and ovules of Holodiscus, Kageneckia, and Porteranthus. Fig. 3.8, Close-up of epitropic, apically inserted Holodiscus ovule (O) with an obturator (Ob) made up of cells from the ventral ovary margin. Fig. 3.9, Dissected Kageneckia flower with files of multiple, pleurotropic ovules (O) in each ovary. Ovules in right-hand ovary are displayed from the funicular side. Fig. 3.10, Close-up of single Kageneckia ovule showing micropyle (arrow) and scar where ovule attaches to margin. Note lack of obturator. Fig. 3.11, Dissected Porteranthus flower with deep floral tube and two basal, apotropic ovules (O) per locule. Fig. 3.12, Close-up of Porteranthus ovules (O) and their funicular obturators (Ob). Sg, stigma; Sy, style; A, stamen; ii, inner integument; oi, outer integument. Scale bars = 100 μm on figs. 3.8, 3.10, and 3.12; 500 μm on figs. 3.9 and 3.11.
insertion in the middle of the ventral margin is typically pleurotropic, although apotropic ovules also occur (figs. 10.44, 10.45). *Holodiscus* ovules are two per locule, epitropic, and inserted at the apical end of the locule on the ventral margin (figs. 3.8, 6.20, 6.21). *Porteranthus* and *Vauquelinia* least resemble the other genera because they have two apotropic ovules per locule positioned near the base of the ventral margin (figs. 3.11, 3.12, 6.26, 6.28, 20.98, 20.99, 21.104, 21.105, 21.107).

Associated with the ovules of all genera examined here, except *Kageneckia* (figs. 3.10, 6.22), is a papillate-celled obturator that varies in its position and association with respect to the ovule funiculus and ovary margin. In most taxa, particularly those with apically inserted, epitropic ovules, the obturator comprises cells from the ventral margin of the ovary wall, as well as from the funiculus of the ovule (figs. 2.4, 2.6, 4.13, 5.16, 10.44, 10.45, 11.51, 14.67, 17.83, 18.88). However, *Holodiscus* obturators are confined to the ventral margin (fig. 3.8), and those of *Porteranthus* and *Vauquelinia* are confined to the funiculus (figs. 3.12, 6.28, 20.97–20.99, 21.105).

**Organogenesis**

*Physocarpus.* Early development of corymbbs in *Physocarpus* occurs in the spring of the year the plant will flower. *Physocarpus* inflorescences are indeterminate or polytelic (Weberling 1989), in that the inflorescence apex does not appear to produce a terminal flower (figs. 7, 8.30). The inflorescence apex produces a succession of bract primordia in a helical, acropetal succession in the axils of which single flowers are initiated (figs. 8.30–8.32). Following bract and flower initiation, flowers develop in an acropetal manner with flowers maturing from the base of the inflorescence (figs. 7, 8.30) even though flowers open simultaneously at anthesis.

Sepal initiation is difficult to determine because of distortion caused by both the proximity of floral apices to one another and compression of the abaxial sepals by inflorescence bracts (figs. 8.32, 8.33). Therefore, it is difficult to determine whether sepal initiation is simultaneous or in a 2/5 phyllotactic pattern (fig. 8.32). Growth of the sepals is initially apical and results in five separate triangular-shaped primordia surrounding the floral apex (fig. 8.33). Intercalary growth below the bases of the sepal primordia results in the floral apex assuming a shallow bowl shape and is the first indication of hypanthium development (fig. 8.34). As the sepals continue to develop, they remain erect and do not enclose the opening of the floral apex until late in development (fig. 11.47).

Petal primordia are initiated simultaneously at the margin of the floral apex and alternate with the developing sepal primordia (fig. 8.33). As the petals develop they are raised above
Fig. 5  Paraffin-embedded sections of mature Aruncus and Chamaebatiaria flowers. Fig. 5.16, Longitudinal section of female Aruncus flower showing unitegmic, epitropic, and apically inserted ovules (O). Note band of nectariferous tissue (Ne) around base of ovaries. Fig. 5.17, Transverse section of female Aruncus ovaries at point of ovule (O) insertion. Ovary suture is closed by the appression of adjacent ventral margin walls as depicted by the darkly stained epidermal cells (arrowhead). Fig. 5.18, Longitudinal section of Chamaebatiaria ovary with multiple, epitropic, and apically inserted ovules (O). Note basal connation of ovaries (arrowhead) and adnation of ovary to hypanthium (arrow). Fig. 5.19, Transverse section of Chamaebatiaria ovary at point of ovule (O) insertion. Ovary is closed by appression of the two ventral margins (arrowhead). N, nucellus; Ob, obturator; A, stamen; H, hypanthium; Ne, nectary. Scale bars = 100 µm on figs. 5.16, 5.17, and 5.19; 500 µm on fig. 5.18.

the bowl-shaped floral apex by intercalary growth of the developing hypanthium (fig. 8.34). Initial development of the petal primordia is both apical and lateral and results in an obovate primordium with a narrow base positioned on the rim of the developing hypanthium (fig. 9.36). As the petals continue to develop apically, they enclose the center of the flower and enclose the organs of the developing androecium and gynoecium (figs. 11.47, 11.48).

Stamen initiation begins with five pairs of stamens on the margin of the concave floral apex (fig. 8.34). Each pair of stamens is anteseptalous and positioned lateral to the petal primordia. Next, a second whorl of five stamens is initiated anteseptally between the members of the first whorl of stamens (fig. 8.35). A third, and final, whorl of five stamens is initiated soon after the second whorl of stamens in an antepetalous position on the concave floral apex (fig. 9.36). Following early development of the gynoecial primordia, the stamen primordia differentiate into a distinct filament and four-lobed anther (fig. 9.40). Initial growth of the stamens is parallel to the floral apex, but as the floral apex widens the stamen filaments turn downward toward the base of the floral cup (figs. 9.39, 9.40).

Soon after initiation of the second whorl of stamens Physocarpus gynoecial primordia are visible in the center of the
floral apex (fig. 8.35). The gynoecium is first visible as a shallow ring primordium in the center of the floral apex (figs. 8.35, 9.36, 11.46). Individual gynoecial primordia are produced by differential growth on the apex of the gynoecial ring primordium (fig. 9.37). As the gynoecial primordia develop, their bases remain connate with each other ventrally (figs. 9.38, 9.39, 11.48). The ventrally connate margins are carried up from the floral apex by intercalary growth as the ovary continues to develop (figs. 9.38–9.40). This results in ovaries that are connate basally, and along their ventral margins, at maturity (fig. 11.50; cf. Schaeppi and Frank 1967, fig. 7). The ventral suture of each ovary, however, is closed by the appression of the ventral margins of each ovary (figs. 11.49, 11.50; cf. Schaeppi and Frank 1967, fig. 7). Each gynoecial primordium differentiates a distinct style and ovary (figs. 9.39, 11.48), with the flattened apex of the style becoming the stigmatic surface of the mature pistil (figs. 9.39, 11.48).

Initiation of ovules in Physocarpus follows the differentiation of the gynoecial primordia into distinct ovaries and styles (fig. 9.40). Typically, two pairs of collateral ovules are initiated acropetally from placentas on the inturned margins of the developing ovary (figs. 9.40, 9.41, 11.48, 11.49). Although initiation of two pairs of ovules was observed consistently, many ovaries may contain only two or three ovules later in development (figs. 10.44, 10.45). Whether this is due to a lack of initiation, the abortion of ovules early in their development, or a combination of both, is not clear (cf. figs. 10.42–10.45). As the ovules develop, inner and outer integuments are initiated below the nucellus (figs. 10.42, 10.43). At this point cells along the inner ventral margin of the ovary appear papillate, signaling the development of the marginal obturator (fig. 10.43). Early in their development the funiculi of adjacent ovules turn away from each other so that the developing ovules are positioned parallel to the floral apex (figs. 10.42, 10.43). This may result in the pleurotropic positioning of ovules at maturity (figs. 10.44, 11.50, 11.51). Development and growth in ovaries that contain only two ovules can be quite variable. In some cases the funiculi of the two ovules bend toward the base of the locale, resulting in apotropic ovules (fig. 10.45). Why this variation in ovule number and positioning occurs is not obvious from the flowers examined in this study, but it may be related to space available in the developing ovary. The outer integument encloses the inner integument and nucellus of the mature ovule, while papillate obturators are visible on both the funiculus and ventral margin (figs. 10.44, 10.45, 11.51).

**Sorbaria.** In contrast to the racemose inflorescence of Physocarpus, the inflorescence of Sorbaria is paniculate (fig. 7). Inflorescences of Sorbaria develop by midsummer conversion of terminal and axillary meristems into inflorescence meristems. The inflorescence meristem initiates bracts in a helical phyllotactic arrangement, in the axes of which primordia are initiated that may become secondary inflorescence meristems (figs. 7, 12.52, 12.53). These secondary meristems initiate bracts in a helical phyllotactic pattern similar to that of the primary meristem. These primordia form floral apices (fig. 12.54) or inflorescence apices (fig. 12.55) depending on their proximity to the primary inflorescence meristem (figs. 12.55–12.57). In all cases development along primary and secondary inflorescences is acropetal (figs. 12.53, 12.56). If the secondary meristem forms a floral apex, two bracteoles are initiated laterally on the apex, in the axes of which two axillary floral meristems form (fig. 12.54). Following initiation of primary bracts, terminal meristems (primary or secondary) develop into flowers whose development is greatly accelerated (figs. 12.56, 12.57). Because the apical meristem of an inflorescence axis differentiates into a flower, Sorbaria inflorescences are classified as determinate, or monotelic (fig. 7; sensu Weberling 1989).

Sepal initiation on floral meristems (terminal or lateral) occurs soon after initiation of the bracteoles. Sepal primordia are initiated in a 2/5 phyllotactic pattern with the first sepal positioned adaxially and opposite the bract (figs. 12.56, 13.58). Initial growth of the sepal primordia is apical and results in a ring of triangular primordia surrounding the floral apex (fig. 13.58). Although the sepals are initiated as separate primordia, their bases become continuous by intercalary growth below their points of insertion; this is the first indication of hypanthium development and results in the floral apex appearing bowl shaped (figs. 13.58, 13.59). Sepals remain more or less erect throughout their development and enclose the floral apex following the initiation and early development of the gynoecial primordia (fig. 15.68).

Petal primordia in Sorbaria are evident on the flattened floral apex during the early development of the sepal primordia, usually before the fifth sepal primordia has completely developed (fig. 13.58). The petal primordia are initiated simultaneously, and in positions that alternate with the developing...
Fig. 7  Diagrammatic representations of early inflorescence development in “Spiraeoideae”

Sepal primordia (fig. 13.58). Petal primordia are also elevated by early development of the hypanthium and appear at the edge of the floral meristem (figs. 13.59–13.61). Petal primordium development is both apical and lateral and results in spatulate-shaped primordia that are connected to the edge of the hypanthium by a narrow base (figs. 13.61, 13.62). As the petals continue to enlarge, they enclose members of the developing androecium and gynoecium (figs. 13.63, 15.68, 15.69).

The first whorl of stamens is made up of five antesepalous pairs on the margin of the concave floral apex (fig. 13.59). The second whorl of stamens to be initiated is a whorl of five stamens below the developing petals and on the edge of the upturned floral apex (figs. 13.60, 13.61). Although 25–30 stamens were observed in mature Sorbaria flowers (table 3), observations of subsequent whorls of stamen primordia were obstructed by development of the gynoecium (figs. 13.61, 13.62). As the stamen primordia continue to develop they differentiate a distinct filament on the end of which a four-lobed anther develops (fig. 14.65).

Initial development of the gynoecium in Sorbaria, as in Physocarpus, comprises a shallow ring primordium in the center of the floral apex (fig. 13.60). Differential growth on the ring primordium leads to the development of five separate primordia that remain connate at their ventral bases (figs. 13.61, 13.62). As the primordia enlarge, their ventral margins remain connate, and their dorsal surfaces appear continuous with the developing hypanthium (figs. 13.62, 13.63, 15.68, 15.69). Intercalary growth results in the ventral ovary margins being connate for half the length of the ovary at maturity (figs. 15.72, 15.73; cf. Schaeppi and Frank 1967, fig. 5; Kania 1973, fig. 18). Following the onset of ovule initiation, the dorsal portion of each ovary continues to be elevated by the elongating hypanthium and at maturity the bottom of each ovary is adnate with the hypanthium (figs. 14.65–14.67, 15.68, 15.70, 15.73; cf. Schaeppi and Frank 1967, fig. 5; Kania 1973, figs. 18, 19). Sorbaria ovaries, like those of Physocarpus, are closed at the point of ovule insertion by the appression of adjacent ventral ovary margins (fig. 15.71). Furthermore, mature Sorbaria ovaries also contain a partial false locular septum on the inner dorsal ovary wall (fig. 15.72).

Ovule initiation begins with the development of a large placenta on the ventral margins of each gynoecial primordium. Four to six ovules are initiated simultaneously on each placenta (fig. 14.64). Initial growth of the ovules is perpendicular to the placenta (fig. 14.65), but later in development the ovules bend away from one another and toward the ventral ovary margin (fig. 14.65). By the time outer integuments are visible the ovules have turned toward the top of the locule, and the base of the funiculus appears swollen where the obturator will develop (fig. 14.66). At maturity the ovules are epitropic and their nucellus and two integuments are notably elongate. Intercalary growth in the ovary wall below the insertion point of the ovules raises them to the upper half of the locule (figs. 14.67, 15.69, 15.70). Adjacent to the micropyle of each ovule...
Fig. 8 Scanning electron micrographs of inflorescence and early floral development in *Physocarpus*. Fig. 8.30, Early inflorescence with acropetally developing floral apices (*fa*) developing in the axils of bracts (*B*). Fig. 8.31, Apical view of inflorescence meristem (*im*). Bract primordia (*B*) are initiated in a basipetal, helical phyllotactic pattern. A recently initiated floral apex (*fa*) is visible in the axil of the second last bract to be initiated. Fig. 8.32, Abaxial view of developing floral apex with sepal primordia (*K₁,...,₅*) initiated in a 2/5 phyllotactic pattern; *Br*, removed bract. Fig. 8.33, Abaxial view of floral apex following the initiation of five petal primordia (*C*). Fig. 8.34, Abaxial view of floral apex following the initiation of the first whorl of 10 antesepalous stamen primordia (*A₁*). Note presence of developing hypanthium (*H*). Fig. 8.35, Abaxial view of dissected flower with second whorl of five antesepalous stamen primordia (*A₂*) initiated between the members of the first whorl (*A₁*). Note shallow gynoecial ring primordium (*G*) in center of floral apex. *C*, petal; *H*, hypanthium; *K*, sepal. Scale bars = 50 µm.
Fig. 9 Scanning electron micrographs of stamen initiation, gynoecium initiation, and early ovule development in Physocarpus. Fig. 9.36, Abaxial view of dissected flower following the initiation of the third, and final, whorl of stamens (A3). Note the shallow ring primordium in the center of the floral apex that signals the development of the gynoecium (G). Fig. 9.37, Development of individual gynoecial primordia (G) through differential growth on the apex of the gynoecial ring primordium. Petals have been removed. Fig. 9.38, Gynoecial primordia (G) following the initiation of a furrow in their ventral face that will develop into the ovary locule. Note continuity of the primordia along their bases (arrowheads); A, stamen. Fig. 9.39, Early development of stigma (Sg), style (Sy), and ovary (Ov) and closure of the ventral furrow. Note that the bases of the ovaries remain continuous (x); A, anther. Fig. 9.40, Dissected ovary following the initiation of two ovules (O) from a basal placenta (pl) on the ventral margin of the ovary; A, anther. Fig. 9.41, Close-up of dissected ovary to show acropetal initiation of ovules (O) on the basal placenta (pl). A1, first whorl of stamens; A2, second whorl of stamens; A3, third whorl of stamens; C, petal; K, sepal; Sy, style. Scale bars = 50 μm.
is a large papillate obturator made up of cells from the funiculus and ventral margin (figs. 1, 14.67, 15.70).

**Spiraea.** Inflorescence development in *S. trilobata* is comparable to that described for *Physocarpus* (figs. 7, 16.74, 16.75). First visible in the spring of the season the plant will flower, the inflorescence meristem initiates bracts in a helical phyllotactic pattern in the axil of which a single floral meristem develops (fig. 16.74; Payer [1857] 1966; Kania 1973). When the inflorescence meristem ceases to initiate bracts it does not form a terminal flower as observed in *S. sorbifolia* but instead leaves an apical residuum on the apex of the inflorescence (figs. 16.74, 16.75). Therefore, the mature inflorescence of *S. trilobata* is classified as indeterminate, or polytelic sensu Weberling (1989). The mature inflorescence of *S. alba*, whose development was not examined here, is a panicle (table 2). Like *Physocarpus*, bracteoles are not initiated on the margin of *S. trilobata* floral meristems, and therefore the next floral organs to initiate are the sepals (fig. 16.76).

The sequence of sepal primordia is difficult to determine because of the rapid sequence of organ initiation (fig. 16.74). Three sepals, one adaxially and two adaxially, appear to develop simultaneously on the floral apex (figs. 16.74, 16.76). This is followed by the initiation of two lateral sepal primordia (figs. 16.74, 16.76). The five sepal primordia remain separate during their early development, but intercalary growth below their common bases causes the young floral apex to appear

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**Fig. 10** Ovule development within *Physocarpus*. Fig. 10.42, Abaxial view of four ovules following initiation of inner (ii) and outer (oi) integuments. Fig. 10.43, Abaxial view of dissected ovary with only three developing ovules. Fig. 10.44, Mature ovary with three pleurotropic ovules (O). Note papillate marginal obturator (Ob). Fig. 10.45, Abaxial view of two mature ovaries from the same flower. Note variation in position and number of ovules (O) between the two ovaries. Ovules in the right-hand ovary are inserted on the middle of the ventral ovary margin and apotropic. ii, inner integument; oi, outer integument; N, nucellus; Ob, marginal obturator; m, micropyle. Scale bars = 50 μm on figs. 10.42, 10.43; 100 μm on figs. 10.44, 10.45.
bowl shaped and is the first indication of hypanthium development (fig. 16.77). Apical growth of the sepals, as well as elongation of the hypanthium, causes the sepals to enclose the other developing floral organs later in development (fig. 18.85).

After the initiation of the sepal primordia, five petal primordia are initiated simultaneously on the edge of the floral apex and alternate with the five sepal primordium (fig. 16.76). Intercalary growth of the hypanthium places the petal primordia on the edge of the developing hypanthium above the level of the floral apex (figs. 16.77, 18.84). Early growth of the petal primordia, like those of *Physocarpus* and *Sorbaria*, is from the apex and lateral margins, leaving the base of the petal narrow where attached to the rim of the hypanthium (figs. 16.79, 18.85). Continued growth of the hypanthium results in the petals, like the sepals, being positioned on the rim of the hypanthium above the other androecium and gynoecium, and enclosing the center of the floral apex (fig. 16.79).

The first whorl of stamen primordia is made up of five pairs of antesepalous primordia initiated at the margin of the con-
Fig. 12 Scanning electron micrographs of inflorescence and early floral development in Sorbaria. Fig. 12.52, Apical view of inflorescence with primary (1°) and secondary (2°) inflorescence apices. Fig. 12.53, Close-up of 1° inflorescence apex initiating bract primordia (B) in a basipetal helical pattern, in the axil of which a primordium (p) is initiated. Fig. 12.54, Close-up of axillary floral apex (fa) early in its development. Two bracteoles (b) have been initiated from its lateral flanks. Initiated in the axil of each bracteole is a single primordium (p). Fig. 12.55, Close-up of secondary inflorescence apex (2°) following the initiation of bracts (B) with primordia (p) in their axils. Fig. 12.56, Terminal portion of inflorescence following differentiation of 1° inflorescence apex into a floral apex (tfa). Note the acropetal decrease in the number of floral apices (fa) visible in each bract (B). Fig. 12.57, Close-up of axillary inflorescence branch showing precocious development of terminal flower. b, bracteoles; fa, floral apex; B, removed bract; K, sepal. Scale bars = 100 μm.
Fig. 13 Scanning electron micrographs of early floral organ primordia development and gynoecial differentiation in *Sorbaria*. Fig. 13.58, Abaxial view of floral apex following initiation of five petal (C) primordia; K₁₋₅, sepals. Fig. 13.59, Abaxial view of dissected floral apex following the initiation of the first whorl of 10 antesepalous stamens (A₁). Note early development of the hypanthium (H). Fig. 13.60, Abaxial view of floral apex following the initiation of a second whorl of five stamens (A₂) that are positioned antepetalously. Note the shallow gynoecial ring (G) in the center of the floral apex. Fig. 13.61, Abaxial view of floral apex following the differentiation of individual gynoecial primordia (G) from the gynoecial ring. Fig. 13.62, Abaxial view of gynoecial primordia (G) later in development. Their ventral bases remain connate, and their dorsal margins are adnate to the developing hypanthium (arrowhead). Fig. 13.63, Abaxial view of gynoecium following development of a furrow in the ventral face of each gynoecium. Note basal connation (arrow) and dorsal adnation (arrowhead) to hypanthium (H) of the gynoecium. A₁, first whorl of stamens; A₂, second whorl of stamens; Cr, removed petal; A, stamen; C, petal; K, sepal. Scale bars = 25 μm.
Fig. 14  Scanning electron micrographs of ovule initiation, development, and morphology in Sorbaria. Fig. 14.64, Longitudinally dissected ovary with large placenta (pl) reaching into locule. On the most dorsal portion of the placenta four to five ovule primordia (O) can be observed. Fig. 14.65, Abaxial view of dissected ovary with developing ovules. Both the nucellus (N) and inner integument (ii) are visible on the curved ovule primordia. Fig. 14.66, Dissected ovary with ovules now possessing an outer integument (oi) and first signs of a funicular obturator (Ob). Note basal adnation of ovary to hypanthium (H). Fig. 14.67, Dissected mature ovule whose basal third is completely adnate to the hypanthium (H). Note apical insertion of the multiple epitropic ovules (O) and obturators (Ob) made up of papillate cells from funiculi and ventral ovary margin. A, stamen; H, hypanthium; Sg, stigma; Sy, style; ii, inner integument; N, nucellus. Scale bars = 50 μm on fig. 14.64; 100 μm on figs. 14.65–14.67.

cave floral apex, alternating with each of the five petal primordia (figs. 16.77, 18.84). At the time of stamen initiation the floral cup is well developed as a result of elongation of the hypanthium, and therefore the first whorl of stamen primordia appears to be initiated on the inner surface of the hypanthium. The second whorl of stamen primordia also appears to be initiated on the inner surface of the developing hypanthium and is made up of five antepetalous primordia (fig. 16.78). The position of the third whorl of stamens is difficult to determine because petal and stamen primordia obscure the margin of the floral apex (fig. 16.78). Payer ([1857] 1966) represented the initiation of secondary and tertiary stamen whorls in Spiraea laevigata as simultaneous. Kania (1973) observed that the 40 stamens of Spiraea salicifolia initiated in four successive whorls: five antesepalous pairs and three whorls made up of both antesepalous and antepetalous stamens.

The initiation of gynoecial primordia in Spiraea differs from that observed in Physocarpus and Sorbaria as discrete gyn-
Fig. 15  Resin- and paraffin-embedded sections of *Sorbaria* gynoecium and ovule development. Fig. 15.68, Longitudinal section through flower whose ovaries have initiated large basal placenta (pl). Note axillary flower showing early differentiation of gynoecial primordia from gynoecial ring (G). Fig. 15.69, Longitudinal section through two ovaries following initiation of ovule primordia (O) on placenta (pl). Intercalary growth below the developing ovules places them in the upper portion of the locule. Note early differentiation of stigmatic surface (Sg) on top of style (Sy). Fig. 15.70, Longitudinal section through mature ovary that is connate along its ventral margin and adnate to the hypanthium (H) near its base. Multiple bitegmic, epitropic ovules (O) are positioned near the top of the locule. Darkly staining papillate cells of the funicular marginal obturator (Ob) are also visible. Figs. 15.71–15.73, Transverse sections through mature ovaries. Fig. 15.71, Section through top of ovule (O) insertion. The ovaries are free from one another and the hypanthium at this point. Ovary sutures are closed by the appression of adjacent ovary margins (arrowhead). Fig. 15.72, Transverse section through middle of ovary. Ventral margins of ovaries are completely connate. Dorsally the ovaries are free of the hypanthium. Note partial false locular septum on inner dorsal wall of locule (arrow). Fig. 15.73, Transverse section near base of ovaries where adnation to the hypanthium (H) is first evident. A, stamen; C, petal; H, hypanthium; O, ovule; ii, inner integument; N, nucellus; oi, outer integument; Ob, obturator. Scale bars = 100 μm.

Gynoecial primordia are visible in the center of the floral apex (cf. fig. 16.78 with figs. 9.36, 13.60). During their development the five primordia remain separate from one another, as well as from the developing hypanthium (fig. 16.79). This is similar to Payer’s ([1857] 1966) observations of *S. laevigata* (see his figs. 12, 14–21), but Kania (1973) observed basal connation between the gynoecial primordia of *S. salicifolia*. Following the development of a furrow in the ventral face of each primordium (fig. 16.79), each primordium differentiates an apical region that will become the style and stigma and a basal region that will become the ovary (fig. 17.81). At maturity, *Spiraea* ovaries are free from one another and the hypanthium and are closed along their ventral faces by the appression of adjacent margins (fig. 18.89).

Ovule initiation in *Spiraea*, as observed in *Sorbaria*, begins with the differentiation of a large placenta from each ventral
margin that extends into the developing ovary locule (fig. 17.80). Three to four ovule primordia are initiated simultaneously on each placenta (figs. 17.80, 18.86). Initial growth of the ovule primordia is perpendicular to the placenta and toward the interior of the ovary locule (fig. 17.81). Intercalary growth, similar to that observed in Spiraea, develops only a single integument, which encloses the nucellus as it develops (figs. 17.82, 18.87). However, Payer ([1857] 1966) observed the development of two integuments on ovules of Vauquelinia.

Mature ovules of Physocarpus opulifolius (including var. “Luteus”) initiate? No No Following petal initiation Antepetalous After gynoecial primordia Yes Yes

Physocarpus opulifolius

Sorbaria sorbifolia initiate? Yes Yes Following petal initiation Antepetalous After gynoecial primordia Yes Yes

Sorbaria sorbifolia

Spiraea trilobata initiate? No No Following petal initiation Antepetalous After gynoecial primordia No No

Spiraea trilobata

Vauquelinia californica initiate? Yes Yes Following petal initiation Antepetalous After gynoecial primordia Yes Yes

Vauquelinia californica

Following the initiation of bracts the terminal inflorescence meristem differentiates into a floral apex (fig. 19.90). Although development along the inflorescence is acropetal, development of the terminal floral apex appears to be more rapid than surrounding floral apices, as illustrated by the presence of sepal primordia before other flowers in its close proximity (fig. 19.90). Rapid development of terminal flowers has also been observed in Amelanchier (Steeves and Steeves 1990), Exocorda, Oemleria, and Sorbaria (figs. 12.56, 12.57; Evans and Dickinson 1999).

Sepal initiation in Vauquelinia follows a 2/5 phyllotactic pattern with the first sepal initiated adaxially on the flattened floral apex (figs. 19.90, 19.91). Sepal primordia quickly enlarge both laterally and apically, enclosing the developing floral apex early in its development (fig. 21.101).

Five petal primordia are initiated at the edge of the floral apex (fig. 21.100) and alternate with the five sepal primordia (fig. 19.92). Following early growth of the hypanthium, the sepals, petals, and stamen primordia of the first whorl are situated well above the cup-shaped floral apex (fig. 19.92). As the petal primordia continue to develop, their bases remain narrow where attached to the hypanthium, while their apical and lateral portions continue to enlarge (figs. 19.92, 19.93).

The first whorl of stamen primordia are five antepetalous and appear to be initiated from the developing hypanthium as a result of intercalary growth below the sepals, petals, and first whorl of stamen primordia (fig. 19.93). Initiation of the second whorl of stamens occurs antepetalously and appears to coincide with the initiation of the gynoecium (fig. 19.93). Initiation and early development of the third whorl...
of stamens is obscured by development of the gynoecium and first two whorls of stamens (fig. 19.94).

The gynoecium of *Vauquelinia*, like those of *Physocarpus* and *Sorbaria*, initially appears as a shallow ring primordium in the center of the floral apex (fig. 19.93). Five individual primordia arise from the ring primordium through localization of growth on its summit (figs. 19.94, 21.101). The gynoecial primordia remain connate along their ventral bases because of intercalary growth below the primordia, and are also adnate to the developing hypanthium along their dorsal surfaces (figs. 19.94, 19.95). Early development of the ovary locale is indicated by a furrow forming in the ventral face of each gynoecial primordium (fig. 19.95). Further development of the gynoecial primordia gives rise to a style topped by a flat-topped stigma and a basal ovary whose dorsal region remains partially adnate to the hypanthium (fig. 20.96). When mature the ventral-most margins of the five ovaries are connate the entire length of the ovary (figs. 21.106, 21.107), a small file meristem is visible in the center of the floral apex (figs. 21.105, 21.107), and the ventral suture of each ovary is closed by the appression of adjacent margins (figs. 21.106, 21.107).

Ovule development begins with the initiation of two ovule primordia from placentas at the bases of the ventral margins (fig. 20.96). As the ovules develop, two integuments are initiated below the nucellus (fig. 20.97) and their funiculi bend toward the floral apex (figs. 20.97, 21.103). A funicular obturator develops just below the nucellus and integuments (figs. 20.97, 20.98, 21.103). Mature ovules are apotropous at maturity (figs. 20.99, 21.105) and, although quite elongate, have a small nucellus positioned at the base of the ovule (fig. 21.105). The large integuments form the seed wing following fertilization (Hess and Henrickson 1987).

**Discussion**

To examine hypotheses concerning relationships of the “Spiraeoideae,” this study has compared the mature floral morphology of 10 genera and floral ontogeny of four of these genera. Previous analyses of phytochemistry (Challice 1974, 1981), morphology (Hutchinson 1964; Kalkman 1988), wood anatomy (Zhang 1992), and DNA sequences (Morgan et al. 1994; rbcL: Morgan et al. 1994; nrITS: Campbell et al. 1995) demonstrate that genera traditionally placed in “Spiraeoideae,” or tribes within this subfamily, do not form monophyletic assemblages.

Although many studies regard some of the taxa traditionally placed in “Spiraeoideae” as the ancestral stock of the Rosaceae (Hutchinson 1964; Sterling 1966a, 1966b, 1969; Challice 1974, 1981; Kalkman 1988), most did not employ outgroups for character polarization (Maddison et al. 1984). Hutchinson (1964, p. 177) regarded the Rosaceae as being derived from “the same stock as the Dilleniaceae, a woody family almost confined in the tropics.” Thus, he surmised that the most primitive rosaceous tribe should also be tropical and chose the Quillajaeae because it is confined primarily to the tropical Americas. Schaeppi and Frank (1967) determined carpels of the “Spiraeoideae” to be primitive within the Rosaceae on the basis of hypanthium development and gynoecium morphology.

Sterling (1966a, 1966b) observed open ovary sutures, degree of fusion between ovular and wing vascular bundles in the ovary, and ovule integument fusion to conclude that some “Spiraeoideae” are the most primitive within the family. Sterling (1966a, 1966b) observed open ventral sutures in *Aruncus, Chamaebatia*, *Kageneckia*, *Lyonothamnus*, *Physocarpus, Porteranthus, Sorbaria, Spiroa*, and *Vauquelinia*. All taxa in the present study, except *Holodiscus*, have ovaries that are closed by appression of the epidermal layers of adjacent ovary margins (table 3; figs. 5.17, 5.19, 6.24, 6.26, 11.50, 15.71, 18.89, 21.106, 21.107; Schaeppi and Frank 1967).

Zhang (1992) and Morgan et al. (1994), however, used characters derived either from a hypothetical outgroup (“Proto-Rosaceae”: Zhang 1992) or from the rbcL sequence of a number of hypothesized outgroup taxa (Morgan et al. 1994). The results of these analyses place taxa of subfamily Rosoideae as most ancestral in the family and place many “Spiraeoideae” genera sister to more derived taxa in the Amygdaloideae and Maloideae (Schaeppi and Frank 1967; Kania 1973).

**Relationships of Spiraeoid Genera Based on Mature Floral Morphology**

In another study we used comparisons of mature morphology and floral ontogeny, mapped onto a phylogeny based on data from morphology (Kalkman 1988), wood anatomy (Zhang 1992), and rbcL sequences (Morgan et al. 1994) to demonstrate the membership of *Exochorda* in an expanded Amygdaloideae (Evans and Dickinson 1999). We have refrained from a similar exercise for the “Spiraeoideae” because of insufficient floral development data and the uncertainty of the relationships of these taxa within the Rosaceae (see below).

We choose instead to present our morphological and developmental results in the context of previous phylogenetic reconstructions of the Rosaceae.

A phylogeny based on rbcL sequences (Morgan et al. 1994) suggests a close relationship between *Aruncus, Holodiscus,*...
Fig. 17  Scanning electron micrographs of ovule initiation and development in *Spiraea*. Fig. 17.80, Longitudinally dissected ovary with acropetally initiated ovule primordia (O) on a large basal placenta (pl). Fig. 17.81, Dorsal view of two dissected ovaries. Two files of ovule primordia (O) are visible in each ovary. Intercalary growth below the developing ovules in the left ovary has raised them into the upper half of the locule. Note early differentiation of stigmas (Sg) on the flattened apices of the styles (Sy). Fig. 17.82, Dorsal view of two dissected ovaries. Growth of ovule funiculi points the nucellus (N) toward the top of the locule. Only a single integument (I) is visible on each ovule, and obturators (Ob) are beginning to develop at the base of the funiculus. Fig. 17.83, Close-up of dissected multiovulate ovary. Ovules (O) are unitegmic, epitropic, and associated with papillate obturators (Ob) made up of cells of their funiculi and the locule margin. Scale bars = 50 μm in fig. 17.80; 100 μm in figs. 17.81–17.83.

and *Spiraea*. Characters studied here that are potential synapomorphies of *Aruncus*, *Holodiscus*, and *Spiraea* include multiple pistils, closed ovaries, and unitegmic, epitropic ovules that are terminally inserted and associated with an obturator (figs. 2.2–2.4, 2.7, 5.16, 5.17, 6.20, 17.81, 17.83, 18.88, 18.89). Fruit morphology has been used to isolate *Holodiscus* from other spiraeoid taxa (Hutchinson 1964; Schulze-Menz 1964; Kalkman 1988), but Morgan et al. (1994) found fruit type to be less reliable than characters derived from phytochemistry, rust parasites, and base chromosome number for determining relationships in the Rosaceae. Some Rosoideae genera have terminally inserted unitegmic, epitropic ovules (Hutchinson 1964; Evans 1999), but these genera are uniovulate and lack an obturator (Evans 1999). Therefore, a potential Spiraeae should include *Holodiscus*.

Although considered a member of “Spiraeoideae,” the relationships of *Lyonothamnus* within the subfamily are not certain. The results of Morgan et al. (1994) propose a relationship between *Lyonothamnus* and rosoid genera *Cercocarpus* and *Purshia*. This relationship, however, is not strongly supported (three base substitutions, decay index = 1; Morgan et al. 1994). Furthermore *Lyonothamnus* has little in common morphologically with these two genera. Both rosoid genera have single pistils and ovaries with single ovules that are positioned near
Fig. 18  Resin- and paraffin-embedded sections of *Spiraea* floral and ovule development. Fig. 18.84, Longitudinal section of floral apex following initiation of sepals (K), petals (C), and first whorl of antesepalous stamen primordia (A₁). Development of hypanthium is visible below the petal primordium (arrowhead); B, bract. Fig. 18.85, Longitudinal section of floral apex following initiation of gynoecial primordia (G) in the center of the floral apex; A, stamen; C, petal. Fig. 18.86, Longitudinal section of ovary following initiation of ovule primordia (O) on large marginal placenta (pl). Fig. 18.87, Longitudinal section of ovaries with apically inserted ovules following intercalary growth below their point of insertion. Note that only a single integument is visible on each ovule (O); A, stamen. Fig. 18.88, Longitudinal section through mature ovary with multiple unitegmic, apically inserted ovules (O). Individual ovaries are free from one another and inserted on the hypanthium (H) above the floral apex; A, anther; Ob, obturator. Fig. 18.89, Transverse section of ovaries at the point of ovule (O) insertion. Ovary suture is closed by the appression of adjacent ovary margins (arrowhead). Scale bars = 100 μm.

the base of the locule that develop into achenes (Hutchinson 1964). Detailed information about ovary and ovule morphology, and the presence of an obturator, are not available for these taxa because they have not been sampled in the current study (Evans 1999). *Lyonothamnus*, however, is multi-pistillate (fig. 4.14); has ovaries that are basally connate and adnate to the hypanthium; has multiple bitemgic, epitropic ovules that are terminally inserted and associated with obturators (fig. 4); and has a dehiscent follicle fruit (Kalkman 1988). These characters are also present in two taxa of the Sorbariae, *Chamaebatiaria* and *Sorbaria*, and have led to the inclusion of *Lyonothamnus* in this tribe (Schulze-Menz 1964; Sterling 1966b). However, the results of Morgan et al. (1994) show strong support for the separation of *Lyonothamnus* from these two genera. Although *Lyonothamnus* flowers appear similar to those of *Chamaebatiaria* and *Sorbaria*, it has been described as an isolated member of the spiraeoid complex (Goldblatt 1976; Morgan et al. 1994; Takhtajan 1997). Therefore, more data will be required to determine an accurate position for *Lyonothamnus* within the Rosaceae.

Another spiraeoid-rosoid relationship inferred from the analysis of Morgan et al. (1994) is the strongly supported (six base substitutions, decay value = 5) clade made up of *Adenostoma*, *Chamaebatiaria*, and *Sorbaria*. The gynoecium of *Adenostoma* is composed of a single pistil that is free of the hypanthium with an ovary that contains a single apically inserted bitemgic, epitropic ovule associated with a marginal obturator (Evans 1999) that becomes an achene. *Chamaebatiaria* and *Sorbaria* gynoecia comprise multiple pistils with ovary sutures that are closed by appression and basally connate ovaries that are adnate to the hypanthium along the bottom third of the ovary. Their ovaries, which later develop into
follicles, contain multiple apically inserted bitegmic, epitropic ovules with obturators comprised of cells from the funiculus and ventral margin of the ovary wall (figs. 2.5, 2.6, 5.18, 5.19, 14.67, 15.70–15.73). Thus, an alliance between these three taxa would require reductions in both pistil and ovule number, the loss of ovary-hypanthium adnation, and the hypothesis that achenes represent a case of convergent evolution within the Rosaceae (Morgan et al. 1994).

Physocarpus is the only genus of traditionally circumscribed Neilleia collected for analysis (table 2). Results from the rbcL analysis of Morgan et al. (1994) place Physocarpus as sister taxon to Neillia as per traditional tribal classifications (Hutchinson 1964; Schulze-Menz 1964). Neillia gynoecia are made up of one to two sessile pistils, each with several (five to 10) ovules (Rehder 1940; Hutchinson 1964; Schulze-Menz 1964). Physocarpus gynoecia comprise a variable number of pistils (table 3) whose ovaries are connate from the base to partway up the ovary (fig. 11.50) and contain a variable number of ovules whose position appears to be dependent on ovule number (figs. 10.44, 10.45, 11.50). The results obtained here appear to support the close relationship of these two taxa, but micromorphological analyses of Neillia would provide additional data with which to test this hypothesis.

Although suggested earlier on the basis of floral characters (Stebbins 1958; Sterling 1966b) and base chromosome number (Goldblatt 1976; Thorne 1983), the results of Morgan et al. (1994) were the first to place Kageneckia (x=17) and Vauquelinia (x=15) within the Maloideae. Kageneckia has multiple pleurotropic, bitegmic ovules that are comparable to those observed in Cydonia and Chaenomeles (Rohrer et al. 1994; Evans 1999). Kageneckia ovaries are neither connate nor adnate to the hypanthium (figs. 6.22, 6.23), characters present in some members of subfamily Maloideae (Rohrer et al. 1994). Vauquelinia is more malooid-like with ovaries that are connate along their ventral margins and basally adnate to the hypanthium at their base (figs. 21.105–21.107; Hess and Henrickson 1987). Moreover, each ovary contains a pair of collateral bitegmic, apotropic ovules, each of which is associated with a funicular obturator (figs. 20.99, 21.105; Hess and Henrickson 1987). These characters would appear to provide evidence for the inclusion of both Kageneckia and Vauquelinia within an expanded Maloideae.

Porteranthus, a genus not included in previous phylogenetic studies of the Rosaceae, is traditionally placed in tribe Gilleniae with Chamaeabatiaria and Sorbaria (Hutchinson 1964). Chamaeabatiaria, Sorbaria, and Porteranthus have ovaries that are connate at the base and ventral sutures that are closed by appression of the ventral margin epidermal layers (figs. 5.18, 5.19, 6.26–6.28, 15.70–15.73). Chamaeabatiaria and Sorbaria ovaries are adnate to the hypanthium and enclose multiple apically inserted epitropic ovules that are associated with obturators made up of cells from both the ovary margin and ovule funiculi (figs. 2.6, 5.18, 14.67, 15.70). Porteranthus ovaries are free of the hypanthium and contain pairs of basally inserted bitegmic ovules, each with a funicular obturator (figs. 3.12, 6.28). The ovule characters observed in Porteranthus are typically observed only in flowers of Vauquelinia and most Maloideae (Hess and Henrickson 1987; Steeves et al. 1991; Evans 1994, 1999, Rohrer et al. 1994). Furthermore, analyses of morphology and the chloroplast gene ndhF data sets place Porteranthus within an expanded Maloideae and sister to Kageneckia and Vauquelinia (Evans 1999). These recent results are significant because Porteranthus has a base chromosome number of x=9, thus providing corroborating evidence for the hypothesis that the Maloideae originated from a spiraeoid ancestor (Gladkov 1972; Cronquist 1981), rather than a paleohybridization event between spiraeoid and amygdaloid ancestors (Sax 1933; Stebbins 1950, 1958; Challice 1974, 1981; Pipps et al. 1991; Rohrer et al. 1991; Morgan et al. 1994).

Comparative Ontogeny of Inflorescences and Flowers

Our analysis of floral ontogeny in “Spiraeoideae,” although limited to four genera, has allowed us to determine homologies for mature floral structures used in the comparisons above and to observe features of floral ontogeny that are comparable to those found in studies of Maloideae and Amygdaloideae. Inflorescence development in the four taxa studied here included simple inflorescences in Physocarpus opulifolius and Spiraea triloba. In both taxa single floral apices were initiated in the axils of basipetally initiated bracts (figs. 8.30, 8.31, 16.74, 16.75). Furthermore, the inflorescence apex, upon completion of bract initiation, did not terminate in a floral apex but in an apical residuum (figs. 16.74, 16.75; table 4). In both taxa bracteoles were not initiated laterally on the undifferentiated floral apex (figs. 8.31, 8.32, 16.76; table 4). This mode of inflorescence development has also been observed for Prunus virginiana (Evans and Dickinson 1999).

Inflorescences of Sorbaria soriobifolia and Vauquelinia californica, however, are more complex. In Sorbaria multiple inflorescence apices were initiated along the length of the developing inflorescence (fig. 12.52). All secondary inflorescences
apices followed a pattern of development similar to that of the terminal apex (figs. 12.53, 12.55). Upon completion of bract initiation, the inflorescence apex (primary or secondary) differentiates into a floral apex (figs. 12.56, 12.57; table 4). Differentiation of the inflorescence apex into a floral apex also occurs in Amelanchier, Exochorda, and Oemleria (Steeves and Steeves 1990; Evans and Dickinson 1999). Sorbaria inflorescences at anthesis comprise large axillary or terminal panicles. Analyses of inflorescence ontogeny in paniculate species of Spiraea (e.g., Spiraea alba) would be useful.

Inflorescence development in Vauquelinia was less complex than that observed in Sorbaria but involved the initiation of multiple floral primordia in the axil of a single bract and differentiation of the inflorescence apex into a terminal flower (fig. 19.90; table 4). Floral primordium initiation in the axil of each bract resulted in either a three-flowered dichasium or a multifiwered pleiochasium (fig. 7; Rickett 1944, 1955). The initiation of dichasias has also been described for members of Crataegus section Donglasii (Evans and Dickinson 1996) and Rosa setigera (Kemp et al. 1993).

Early floral development in Physocarpus, Sorbaria, Spiraea, and Vauquelinia is more variable than that observed in other rosaceous taxa with respect to sepal and stamen whorl initiation. Sepal initiation in Physocarpus may be simultaneous,
Fig. 21  Paraffin-embedded sections of floral and ovule development in *Vauquelinia*. Fig. 21.100, Longitudinal section of floral apex following initiation of sepal (K) and petal (C) primordia. Fig. 21.101, Longitudinal section of floral apex following initiation of shallow gynoecial ring primordium (G); A, stamen; C, petal; K, sepal. Fig. 21.102, Longitudinal section of floral apex whose gynoecial primordia (G) are dorsally adnate to the base of the hypanthium (H). Fig. 21.103, Longitudinal section of ovary and ovule. Ovule comprised of nucellus (N), two integuments, and funicular obturator (Ob). Note dorsal adnation of ovary with hypanthium. Fig. 21.104, Longitudinal section of mature flower with ovaries adnate to the hypanthium (H) at their base; A, stamen; O, ovule; Sg, stigma; Sy, style. Fig. 21.105, Close-up of ovule in fig. 21.104 with dorsally elongate integuments. Note adnation of ovary to hypanthium and small file meristem (fm) in the center of the ovaries (arrowhead); ii, inner integument; N, nucellus; Ob, obturator; oi, outer integument. Fig. 21.106, Transverse section of top of ovaries. Ovary sutures are closed by appression of adjacent ventral margins (arrowhead). Note connation of ovaries along their ventral margins. Fig. 21.107, Transverse section at point of ovule (O) insertion. Ovary sutures are closed by the appression of adjacent ovary margins (arrowhead). Apex of file meristem (fm) is visible in the center of the ovaries. Note partial false locular septum on the inner dorsal wall of each locule (arrow). Scale bars = 100 μm on figs. 21.100–21.103, 21.106, 21.107; 200 μm on fig. 21.105; 500 μm on fig. 21.104.
but the inflorescence bracts appear to distort the two abaxial stamens (fig. 8.32). *Spiraea* floral apices quickly initiate three sepal primordia (one adaxial and two abaxial) followed by two lateral (fig. 16.76). Additional floral development studies would help determine the extent of variation within spiraeoid taxa. *Sorbaria* and *Vauquelinia* initiate their sepals in a 2/5 phyllotactic pattern. The first whorl of stamens in all taxa is made up of five pairs of antesealous primordia positioned laterally to the petal primordia (figs. 8.34–8.36, 13.59, 16.77, 16.78, and 19.92; table 4; Payer [1857] 1966; Kania 1973; Sattler 1973; Steeves et al. 1991; Kemp et al. 1993; Evans and Dickinson 1996). Initiation of subsequent whorls of stamen primordia is where these taxa differ from other Rosaceae. The second whorl of stamens, made up of five primordia in all taxa, is antesealous in *Physocarpus* and antepetalous in the other taxa. In all taxa studied here the second whorl appears to be initiated at approximately the same time as the gynoecial primordia, with the third whorl appearing after initiation of the gynoecium (figs. 10.44, 10.45) and the remainder basally connate (Evans and Dickinson 1996). Van Heel (1984), however, presents SEMs for *Sorbaria arboarea* (his figs. 25, 26) that resemble gynoecium initiation and early development in *Spiraea* (fig. 16.78). He observed that adjacent ovary margins do not appear continuous until later in development (van Heel 1984, fig. 27). Development of the gynoecium from a ring primordium has previously been described in the genus *Crataegus* (Maloideae: Evans and Dickinson 1996), as well as many other Maloideae flowers (Evans 1999). This character provides additional evidence for the placement of *Vauquelinia* in Maloideae s.l. (Morgan et al. 1994), as well as for the common ancestry of some “Spiraeoideae” and Maloideae.

Adnate of the lower dorsal margin of the ovary with the hypanthium in the development of *Sorbaria* and *Vauquelinia* provides additional evidence for the above hypotheses (figs. 13.62, 13.63, 14, 15.68–15.70, 19.94, 19.95, 20.96, 21.102–21.105; Schaeppi and Frank 1967) and is best represented using the terminology of Leins (1972). Intercalary growth below the insertion of the perianth and androecium is the hypanthium that surrounds, but is free from, the gynoecium in *Physocarpus* and *S. trilobata* (fig. 22; Leins 1972). In *Sorbaria* and *Vauquelinia*, however, the area of intercalary growth extends below the gynoecium (fig. 22). As their hypanthia and ovaries develop, the dorsal margins of the ovaries become adnate to the hypanthium (fig. 22; Leins 1972), a characteristic observed only in the flowers of Maloideae (Rohrer et al. 1994).

All four taxa also differ in the development, insertion, and mature morphology of their ovules. *Spiraea* ovules have a single integument while the others all have bitegmic ovules (figs. 11.51, 15.70, 17.82, 21.105). *Spiraea* and *Sorbaria* initiate multiple ovule primordia from a large basal placenta (figs. 14.64, 17.80). Intercalary growth below the placenta results in their apical insertion within the locale at maturity (figs. 15.70, 18.88; Schaeppi and Frank 1967). *Physocarpus* and *Vauquelinia* ovules are initiated from a small placenta near the base of the ovary (figs. 9.40, 20.96). *Physocarpus* initiates two ovules per placenta, *Vauquelinia* a single ovule per placenta. Intercalary growth below the insertion point of *Physocarpus* ovules positions them in the middle of the locale, but ovule number appears to control their position with respect to each other. When only two ovules are present in the ovary they are apotropic (fig. 10.45). Pleurotropic ovules are typical of ovaries with three (figs. 10.44, 10.45) or four ovules (not shown). Ovules of *Vauquelinia* remain basal throughout development and are apotropous at maturity (figs. 20, 21.103–21.105).

Our comparative analyses of mature floral morphology and floral ontogeny in “Spiraeoideae” and Amygdaloideae further demonstrate the polyphyly of genera traditionally placed in “Spiraeoideae.” These analyses provide additional evidence for the transfer of *Exochorda* to an expanded Amygdaloideae (Goldblatt 1976; Thorne 1992; Morgan et al. 1994; Takhtajan 1997; Evans and Dickinson 1999), as well as the inclusion of *Porteranthus*, *Kageneckia*, and *Vauquelinia* in an expanded Maloideae (Goldblatt 1976; Thorne 1992; Morgan et al. 1994; Campbell et al. 1995; Takhtajan 1997). Our analyses of floral ontogeny in the Amygdaloideae and “Spiraeoideae” are used primarily to determine the homology of mature floral struc-
Structures, but the inclusion of more taxa would provide an alternative data set for phylogenetic analyses, as well as help clarify the variation observed in some larger genera (e.g., *Prunus* and *Spiraea*). An example of the former is the gynoecial ring primordium observed in *Physocarpus*, *Sorbaria*, *Vauquelinia*, and Maloideae (Evans and Dickinson 1996; Evans 1999). This characteristic of gynoecium initiation provides ontogenetic evidence for the common ancestry of some Spiraeoideae and Maloideae, as well as support for the origin of Maloideae from a spiraeoid ancestor. Therefore, floral development data from *Kagenecia* and *Porteranthus* are needed to determine the extent of this particular gynoecial character in Maloideae s.l.

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