

A brief review of the fossil history of the family Rosaceae with a focus on the Eocene Okanogan Highlands of eastern Washington State, USA, and British Columbia, Canada

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Received January 16, 2006; accepted August 17, 2006

Published online: June 28, 2007

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Abstract. Many of the oldest definitive members of the Rosaceae are present in the Eocene upland floras of the Okanogan Highlands of northeastern Washington State and British Columbia, Canada. Over a dozen rosaceous taxa representing extant and extinct genera of all four traditionally recognized subfamilies are known from flowers, fruits, wood, pollen, and especially leaves. The complexity seen in Eocene Rosaceae suggests that hybridization and polyploidy may have played a pivotal role in the early evolution of the family. Increased species diversity and the first appearance of additional modern taxa occur during the Late Paleogene in North America and Europe. The Rosaceae become increasingly important components of fossil floras during the Neogene, with taxa adapted to many habitats.

Key words: Eocene, fossil, Okanogan Highlands, *Prunus*, Rosaceae, temperate floras, Tertiary.

Introduction

The Rosaceae is a large family of approximately 122 genera and 3,370 species of trees, shrubs and herbs of worldwide distribution, with its maximum development in north

temperate regions (Heywood 1993). Members of the Rosaceae have radiated into a wide variety of environments ranging from mesic to xeric communities and are elements of boreal and tundra ecosystems. No doubt one of the driving forces for the Rosaceae's success is the presence of agamospermy, hybridization, polyploidy and vegetative reproduction within the family. All of these microevolutionary processes contribute to generating novel genetic combinations capable of colonizing and persisting in new, open habitats.

It comes as no surprise that the Rosaceae captured the eye of G. Ledyard Stebbins, Jr. Stebbins believed that the subfamily Maloideae (also called the Pyroideae) are allopolyploids that combined adaptive gene complexes derived from ancient lineages of Prunoideae with those from Spiraeoideae (Stebbins 1950, Evans and Campbell 2002). Stebbins suspected that these new complexes had high fitness in new habitats that arose during the middle and late Tertiary. One thing was missing in order for Stebbins' concept to be supported: the fossil evidence.

In October, 1994, Stebbins responded to a letter sent to him by Wes Wehr that was accompanied by a list of rosaceous taxa from Okanogan Highlands floras (DeVore and Pigg 2005; Wesley Wehr Papers at the University of Washington Libraries). Wehr, who died in April, 2004, was Affiliate Curator of Paleobotany at the Burke Museum on the University of Washington campus. In addition to his training in music composition, contributions to the Northwest School of art, and involvement in Seattle's literary scene, Wehr cared for the Burke's extensive collections of Tertiary plant and insect fossils from the Pacific Northwest (Archibald et al. 2005). Stebbins commented in his response to Wehr that "...your information and lists will be most useful to me should I have occasion to publish further communications in this field" (Stebbins, written communication 1994). In fact, Stebbins (1993) did make reference to fossil Rosaceae, in his commentary on the genus *Neviusia* A. Gray. But, the fossil material itself was not formally described until more than ten years later (DeVore et al. 2004). There is no shortage of plant fossils representing the Rosaceae, but there is a shortage of paleobotanists working on deciphering the fossil history of the family.

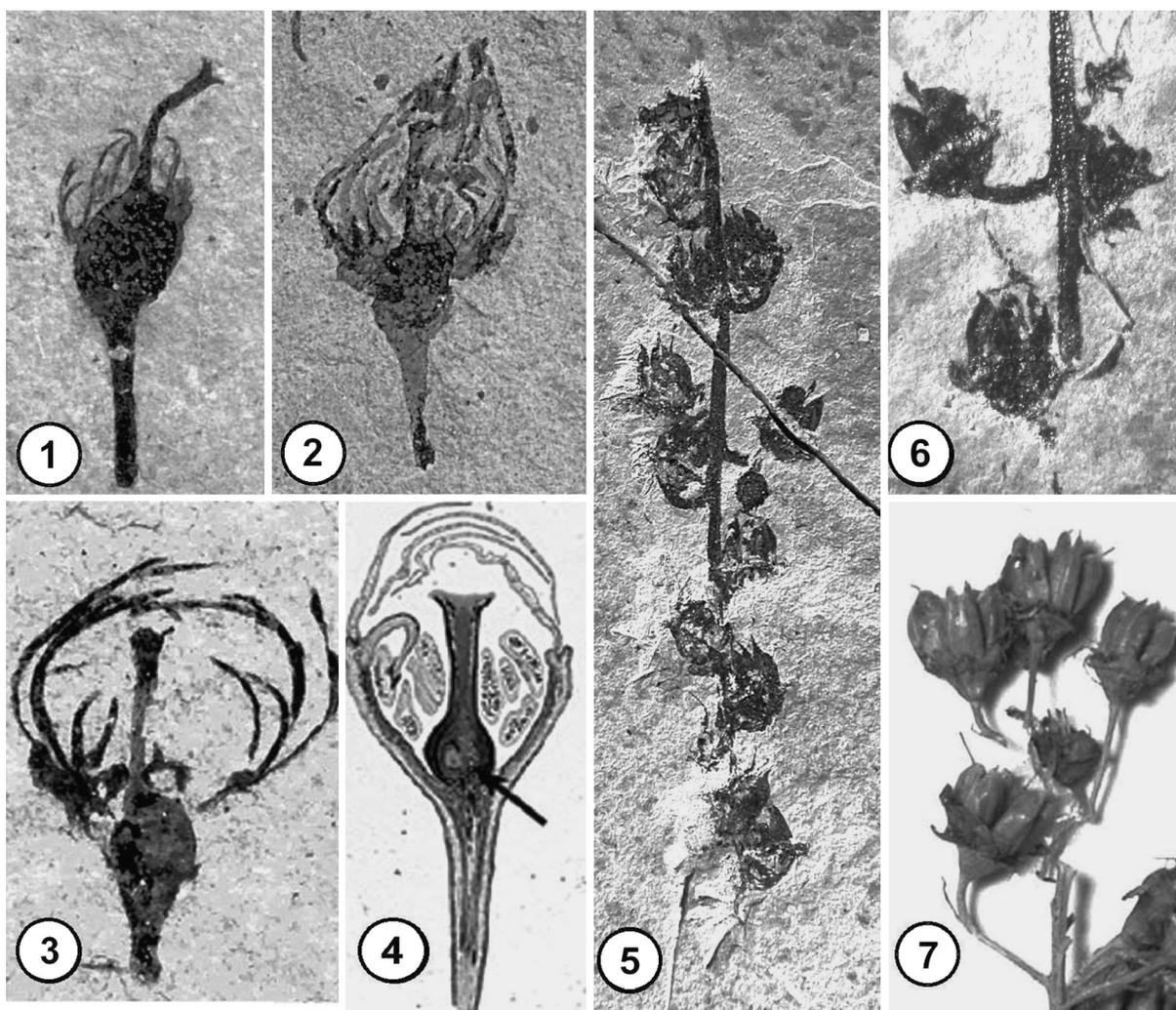
There is indeed a rich fossil record for Rosaceae. The fossil record of rosaceous plants is extensive in North America and Europe from the Eocene on. Neogene rosaceous occurrences are more widespread with reports known in Asia, particularly Japan, the Arctic, several Gondwanan regions, and northern Africa. Fruits, flowers, seeds, pollen, wood and leaves are known from many localities, however, the fossil record has not been well summarized, and therefore has not been readily available to neontologists interested in the family's evolutionary history. In this paper we review the evolutionary history of the Rosaceae as reflected in the fossil record, with a strong emphasis on the North American record, particularly from the Okanogan Highlands. We briefly highlight significant European records, however the interested reader should consult Kirchheimer (1973) and the papers of

Dieter Mai, Zlatko Kvaček and Harald Walther for more detailed discussion (e.g. Mai and Walther 1978; Mai 1984, 1995; Kvaček and Walther 1998, 2001, 2004; Kvaček et al. 2004). This is by no means the end of the story. Numerous rosaceous fossils are nestled within museum cabinets in need of further description. Therefore, this is the story as it stands today and our understanding of the fossil record for Rosaceae will no doubt become clearer once undescribed taxa are critically examined and more widely compared.

The Eocene radiation. The most significant early representation of fossil Rosaceae occurs in the early and middle Eocene floras of central and southern British Columbia, Canada and northeastern Washington state, USA, an area known as the Okanogan¹ Highlands (Figs. 1–16). This region contains a rich fossil flora that differs markedly from contemporaneous floras of southeastern North America and the coastal areas of the Pacific Northwest. The Claiborne Formation of Kentucky and Tennessee has a megathermal flora dominated by lauraceous leaves and legumes (Dilcher 1973), and the Chuckanut and Puget floras of the North Pacific Coast are warm temperate floras with sabal palms (Graham 1999). In contrast, the Okanogan Highlands floras contain both megathermal and temperate elements.

The most diverse of the Okanogan Highlands floras, at Republic, Washington contains a prominent coniferous component (Schorn and Wehr 1986, Wolfe and Wehr 1987), as well as a rich dicot representation (Wehr and Hopkins 1994, Johnson 1996, Wehr and Manchester 1996, Pigg and Wehr 2002, DeVore et al. 2005, Dillhoff et al. 2005, Greenwood et al. 2005). Early evidence of several families and genera that later become prominent members of the cooler temperate floras of the Neogene are found in the Okanogan Highlands floras. Along with the diverse *Acer* L. species (Wolfe and Tanai 1987) and members of Betulaceae

¹ "Okanagan" is the alternative Canadian spelling.

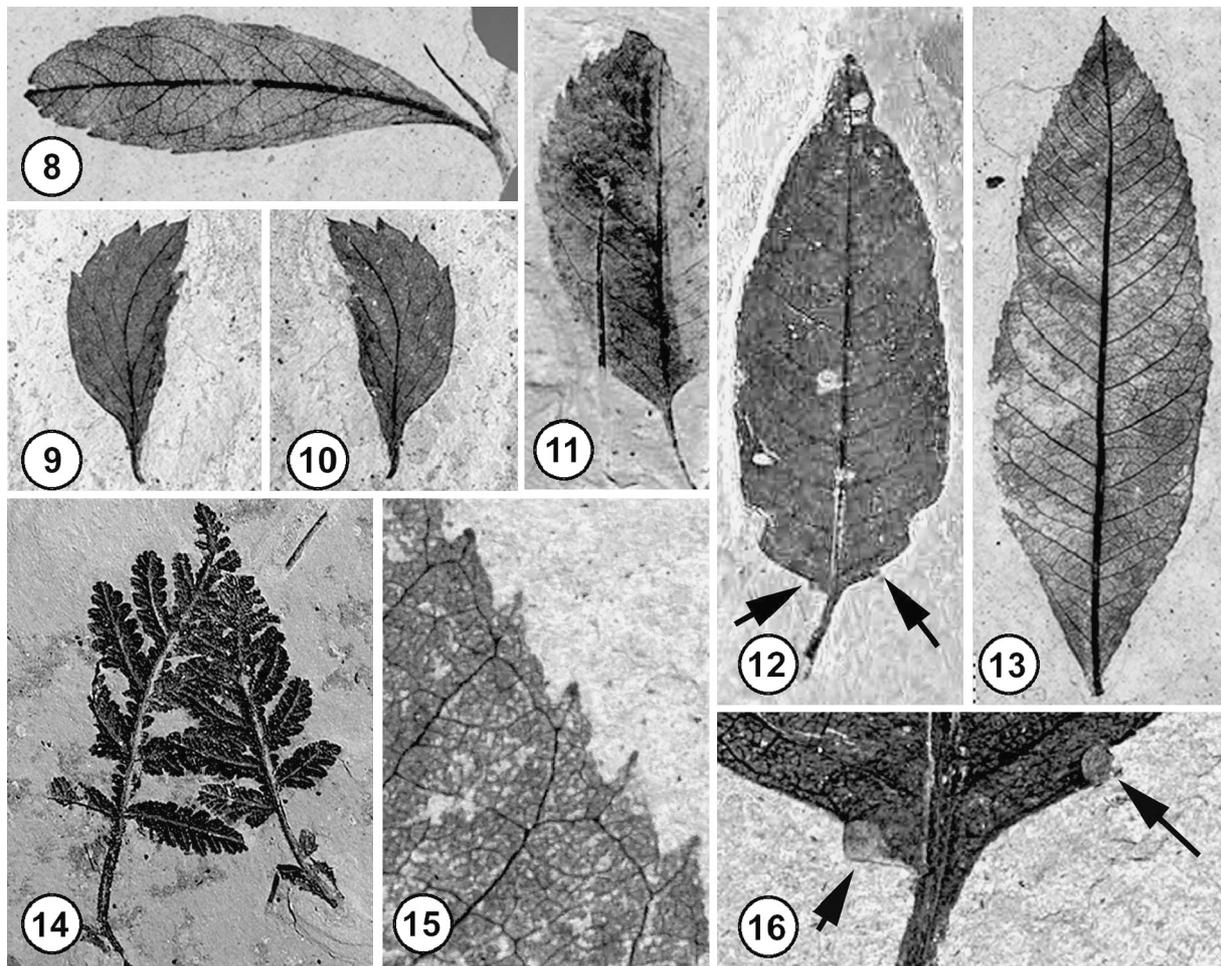


Figs. 1–7. Fossil and extant rosaceous flowers. cf. *Prunus* (1–3) Extant *Prunus* (4) cf. *Spiraea* (5, 6) Extant *Spiraea* (7). **1** *Prunus*-like flower showing ovoid, asymmetric ovary on long pedicel, elongate style with broad stigmatic region, and perianth parts attached to hypanthial rim. Relative size of ovary suggests this specimen may be post-fertilization; SR 96-09-04, x 4; **2** Young *Prunus*-like flower showing gynecium with attached perianth and stamens, SR 96-11-47a, x 3.5; **3** Young *Prunus*-like flower showing gynecium surrounded by perianth parts attached to hypanthial rim; SR 05-05-06b, x 4; **4** Extant *Prunus* flower in longitudinal section, for comparison, x 10; **5** *Spiraea*-like infructescence, UWBM 56785a (B3389), x 4.3; **6** Counterpart of *Spiraea*-like infructescence in Figure 5, showing detail of fruit, UWBM 56785b, x 7.5 (B3389); x 7.5; **7** Extant *Spiraea latifolia* (Ait.) Borkh. fruits for comparison, NYBG

(Crane and Stockey 1987, Pigg et al. 2003), perhaps the most intriguing family in these floras is the Rosaceae.

The rosaceous genera of the Okanogan Highlands floras fall into three general categories: (1). Extant genera that are well established by the Eocene; (2). Eocene forms are

close to, but perhaps not exactly like, extant genera; and (3). Extinct genera with affinities at higher taxonomic levels, such as *Paleorosa* Basinger (Basinger 1976, Cevallos-Ferriz et al. 1993) and *Stonebergia* Wolfe & Wehr (Wolfe and Wehr 1988) which combine characters of several genera or even traditionally recognized



Figs. 8–16. Fossil rosaceous leaves. cf. *Spiraea* (8–10) *Amelanchier* (9) *Prunus* (12, 15, 16); *Photinia pagae* (13); *Stonebergia* 14. 8 *Spiraea*-like leaf with prominent stipule, UWBM 71372b (B2737), x 1.3; 9, 10 Part and counterpart specimen of *Spiraea*-like leaf, UWBM 54112, x 0.9; 11 *Amelanchier*, UWBM 54168 (3389), x 1.3; 12 Overview of *Prunus* leaf showing position of paired basal glands on lamina (arrows), SR 05-05-01a (4131), x 1; 13 *Photinia pagae*, UWBM 71291 (B2737), x 1.5; 14 *Stonebergia* holotype specimen UWBM 54110a, 54111, x 1.4; 15 *Prunus* leaf showing detail of higher order venation and glandular, marginal teeth, SR 00-05-17a, x 5.4; 16. Detail of basal portion of leaf in Fig. 12, showing laminar glands (arrows), SR 05-05-01a (4131), x 3.8

subfamilies. It is not unusual for both extant and extinct taxa to be found side by side in fossil floras of Eocene age (DeVore et al. 2004, 2005). In other situations, the fossils are strikingly similar to their extant counterparts, but may show a wider range of variation or have certain features rare or otherwise unknown for them.

The best known rosaceous genus of the Eocene Okanogan Highlands floras is *Prunus*

L. (including related forms; Figs. 1–3, 12, 15, 16). The first acceptable records of *Prunus* come from these lacustrine deposits and include fruits, wood, and leaves. Additionally, in this paper we illustrate flowers and young fruits from Republic currently under study that are remarkably similar to those of extant *Prunus* (Figs. 1–4). Brown (1962) is often credited with describing the first occurrence of *Prunus* endocarps based on material from

the Paleocene of Colorado. However, Steven Manchester has recently reassessed these fossil fruits and has interpreted them to belong within the family Icacinaceae (S. Manchester, Florida Museum of Natural History, personal communication).

Permineralized *Prunus* endocarps with internal anatomical preservation occur in the Okanogan Highlands Princeton chert of southern British Columbia (Cevallos-Ferriz and Stockey 1991), and in the coeval Clarno Nut Beds of Oregon (Manchester 1994). The endocarps are important because they provide anatomical structure of reproductive organs that can be compared to that of extant cherries. They also provide a fossil record that can be assessed independently from the leaf record. *Prunus* endocarps are quite rare in the Princeton chert, with only a handful of specimens known among the thousands of fossils recovered from this well-studied assemblage (Cevallos-Ferriz and Stockey 1991). They are thought to have been incorporated from “upland” sources, rather than from the autochthonous sediments like the mostly aquatic *in situ* plants (Cevallos-Ferriz et al. 1991, Pigg and Stockey 1996). Cevallos-Ferriz and Stockey (1991) described three forms, all of which show the characteristic apex, endocarp and seed coat layers with the same organization seen in extant *Prunus*. However, these patterns were difficult to relate in detail to extant cherry endocarps since comparative data are not known from all extant groups of this large, cosmopolitan genus. Manchester (1994) reported two species from Clarno: *Prunus weinsteinii* Manchester and *P. olsonii* Manchester. *Prunus weinsteinii* is similar to the endocarp type 1 of the Princeton chert (Cevallos-Ferriz and Stockey 1991), and which Manchester compared with extant *P. avium* (L.) L. Manchester also named *Pruniticarpa cavallosii* Manchester for an endocarp from the Clarno Formation that had similarities with *Prunus* but could not be placed in the genus conclusively. The record of *Prunus* endocarps continues on into the Late Paleogene and Neogene with a range of endocarp

types from Europe (Dorofeev 1963; Kirchheimer 1973; Mai 1984, 1995). These are known primarily from external morphology and not anatomical structure.

Permineralized wood of the traditional subfamily Prunoideae has been found by the Eocene in western North America, the Oligocene of Europe, and the Oligocene-Miocene of Asia (reviewed by Wheeler and Manchester 2002). A unique combination of features that are generically diagnostic of *Prunus* include narrow, numerous vessels that are solitary and in multiples, simple perforations, alternate intervessel pits, heterocellular rays, fibers with distinctly bordered pits, diffuse parenchyma, and traumatic axial canals (Wheeler and Manchester 2002). Wood referred to *Prunus gummosa* (Platan.) Wheeler, Scott & Barghorn is known from western North America in Yellowstone Park (Wheeler et al. 1978), the Princeton chert (Cevallos-Ferriz and Stockey 1990), and the Clarno Formation (Wheeler and Manchester 2002).

A diverse assemblage of *Prunus* leaves is also known from the Okanogan Highlands floras (Wehr and Hopkins 1994, Dillhoff et al. 2005, Greenwood et al. 2005). In addition to sharing typical features of *Prunus* leaf morphology, venation and tooth type (Fig. 15), leaves are recognizable by the characteristic presence of paired glands on the petiole or basal region of the lamina (Figs. 12, 16). Among the hundreds of specimens found, there is a broad range of variation in leaf morphology, with at least five or six general types present.

Along with the *Prunus* leaves from the Republic site, ongoing collecting efforts of the Stonerose Interpretive Center at Republic, Washington, have resulted in the recovery of a group of small rosaceous flowers and young fruit remains. These specimens, which are currently under study (Figs. 1–3) show many features consistent with flowers and young fruits of extant *Prunus* (Fig. 4). These flowers are 1–1.6 cm long, and are attached to an elongate pedicel. Gynoecia have broad, somewhat flattened stigmas similar to those seen in

extant *Prunus* (Figs. 1, 4), elongate styles and an ovoid, somewhat asymmetric ovary (Figs. 1, 3) which one might expect in a drupaceous fruit with a single developing ovule (Fig. 4). Perianth parts are attached along a hypanthial rim (Figs. 1–3) and include several whorls of petals and/or sepals. Anthers are present in at least one flower (Fig. 2), and are folded inward as in extant *Prunus* (Fig. 4). They are being studied for *in situ* pollen.

Another genus for which we have both fertile and vegetative evidence is *Spiraea* L. (Figs. 5, 6, 8–10). One recently discovered infructescence from Republic is 2 cm long with 14 small fruits (Figs. 5, 6), each 2 mm long, that are remarkably like those of extant *Spiraea* (Fig. 7). Beautifully preserved *Spiraea*-like leaves are also known (Figs. 8–10). Interestingly, however, these commonly have prominent stipules (Fig. 8), unlike the extant genus in which they are usually absent.

The most completely known reproductive structures of Rosaceae in the Okanogan Highlands are the anatomically preserved flowers assigned to *Paleorosa*. This flower was first described by Basinger (1976) from the Princeton chert. Additional information was later reported by Cevallos-Ferriz et al. (1993). *Paleorosa* shares features of both the traditional subfamilies Maloideae and Spiraeoideae, with its closest similarities to the firethorn *Pyracantha* M. Roemer (Cevallos-Ferriz et al. 1993), a genus which may also be represented by leaf remains at Republic (W. Wehr, written communication). The Princeton chert thus demonstrates a classic Eocene situation where an extinct genus, *Paleorosa*, occurs in the same strata as a modern genus, *Prunus*.

Paleorosa is significant in containing the oldest known *in situ* rosaceous pollen; isolated pollen is also known in the Eocene of Argentina (Zetter et al. 1999). Eocene pollen with striking rosaceous features was also described *in situ* from floral remains of the genus *Landeenia* Manchester & Hermsen from western North America (Manchester and Hermsen 2000). Interestingly, although its pollen appears rosaceous, other floral features of

this taxon are not consistent with what we currently know about rosaceous flowers. The authors place *Landeenia* in the Sapindales *incertae sedis*. This report reminds us to question the confidence with which we can identify the presence of Rosaceae on the basis of pollen alone.

Another rosaceous reproductive structure from the Clarno Formation is *Quintacava* Manchester (Manchester 1994). Although it cannot be assigned to a modern genus, this anatomically preserved fruit shares similarities with the Maloideae. Wood of the Maloideae is also known at Clarno and may represent the same plant (Wheeler and Manchester 2002). Leaves recognized as *Malus* L./*Pyrus* L. are part of the “Eocene Orchards” at Republic (Wehr and Hopkins 1994). Pollen of *Malus*/*Pyrus* has also been reported from the Late Eocene Florissant locality (Leopold and Clay-Poole 2001).

The majority of Okanogan Highlands rosaceous remains are known not from reproductive structures but from leaves. Although there are limitations, genera with distinctive foliage features can provide significant information. Rosaceous leaves are simple to highly dissected but seldom truly compound, and typically stipulate (Wolfe and Schorn 1990). They typically have brochidodromous secondary venation, “A-O” tertiaries and composite intersecondaries. Leaves are typically toothed, with variably shaped single- or multiple-sized teeth. Teeth typically have weakly developed “rosoid” venation, with a central vein and weak laterals, and often small apical glands.

We recently described *Neviusia dunthornei* DeVore, Moore, Pigg & Wehr, based on leaves from the Okanogan Highlands site at One Mile Creek, British Columbia (DeVore et al. 2004). This is the only fossil record of the small tribe Kerriace, which contains *Neviusia* as its only North American taxon, along with its two Asian relatives *Kerria* (L.) DC. and *Rhodotypos* (Thunb.) Makino. The genus was originally described by Asa Gray from the type species *N. alabamensis* A. Gray from southeastern North America, where it is widespread.

Several years ago, surprisingly, a second species, *N. cliftonii* Shevock, Errter & Taylor was found as a narrowly distributed endemic at Mount Shasta, in northern California (Shevock et al. 1992, Errter 1993, Stebbins 1993). The fossil leaf from One Mile Creek most greatly resembles the California species with its wide leaves with broad teeth, rather than the southeastern *N. alabamensis* which has longer, narrower leaves with smaller teeth.

Photinia pagae Wolfe & Wehr (Fig. 13) was described from the middle Eocene Republic flora of eastern Washington state by Wolfe and Wehr (1987), and a second undescribed species is known from the same flora (Wehr, personal communication 2000). This genus, which is often cultivated as an ornamental has a native Asian distribution today, with 40 species occurring from the Himalayas to Japan and Sumatra.

The oldest evidence of the genus *Amelanchier* Medikus is from the middle Eocene Okanogan Highlands of British Columbia (Fig. 11; W. Wehr, personal communication, 2001). This genus has an extensive fossil record of leaves throughout western North America. Fossil occurrences are relatively common in Eocene and Miocene floras of western North America, and have been reviewed by Schorn and Gooch (1994). *Amelanchier* and *Amalanchites* have been reported from the Paleocene Ravenscrag flora of Saskatchewan (McIver and Basinger 1993), however their identification with Rosaceae has not been verified.

Other rosaceous leaves with first or early occurrences in the Okanogan Highlands include those similar to the widespread genera *Rubus* L., *Crataegus* L. and *Sorbus* L., the eastern Asian *Sorbaria* (DC) A. Braun., and *Pyracantha* today of Europe and Asia. Other extant genera in the Okanogan Highlands floras show the transition into drier habitats. These include the chaparral plants *Hesperomyles* Lindley which is related to extant Central and South American taxa, as well as *Vauquelinia* Baillon. and *Cercocarpus* Kunth. which occur today in southwestern North America.

Stonebergia Wolfe & Wehr (Fig. 14), an extinct genus in the *Chamaebatiaria* (Porter) Maxim. complex is first recognized in the Eocene (Wolfe and Wehr 1988). Additional extinct genera in this group (*Stockeya* Wolfe and Wehr, *Eleopoldia* Wolfe and Wehr) were named from later Eocene and Oligocene floras (Wolfe and Wehr 1988).

Rosaceous genera are also important components of Late Eocene floras in western North America, as characterized by the famous Florissant Formation of Colorado (MacGinitie 1953, Wolfe 1987, Manchester 2001, Meyer 2003). The Florissant flora includes *Rubus*, *Malus*, *Prunus* and possibly *Vauquelinia*. Additionally, this flora has some of the earliest occurrences of *Cercocarpus*, *Crataegus*, *Holodiscus* (K. Koch.) Maxim. (Schorn 1998), *Rosa* L., and leaves referred to *Lomatia* R. Br. Thorns from this locality may also represent *Rosa* (Meyer 2003).

Both leaves and fruits of *Rosa* occur later in the Oligocene Bridge Creek flora of Oregon (Meyer and Manchester 1997), as well as in later Neogene floras of Europe (Mai and Walther 1978; Kvaček and Walther 1998, 2001, 2004; Hably et al. 2000; Kvaček et al. 2004). The European and North American leaf and fruit species of *Rosa* differ, suggesting the North American-European disjunction within this genus today may be of ancient origin (Becker 1963, Mai and Walther 1978, Hably et al. 2000, Tiffney and Manchester 2001).

The Late Oligocene Creede flora of Colorado (Axelrod 1987; Wolfe and Schorn 1989, 1990) has a rich rosaceous component. Among members of Spiraeoideae are the Eurasian genus "*Eleiosina* Raff." (= *Sibiraea* Maxim.), *Holodiscus*, and the extinct genera *Eleopoldia* and *Stockeya*. *Eleopoldia* is closely related to extant herbaceous plants *Luetkea* Bong., *Geum* L., and *Sanguisorba* L., while *Stockeya* is an ancestral relative of the *Chamaebatiaria* group. Other rosaceous genera include *Sorbus*, *Crataegus*, *Potentilla*, *Cercocarpus* (with possible achenes), "*Osmaronia* E. Greene" (= *Oemleria* Reichb.), and rare *Prunus*. Wolfe and Schorn (1989) analyzed the paleoecological distribution

of these taxa in the Creede flora using multivariate statistical techniques and recognized four major plant communities. *Stockeya* was an important member of the mesic juniper woodland community at Creede, while its modern relative, the shrubby desert sweet (*C. millefolium*) inhabits drier high-desert, chaparral sites today. Wolfe and Schorn (1989) concluded that a habitat shift related to modern physiological adaptations occurred in the *Stockeya* lineage prior to morphological change. Several other genera at Creede are closely related to modern-day herbaceous genera, suggesting that a shift from shrubby to herbaceous habit also occurred (Wolfe and Schorn 1989).

Lyonothamnus A. Gray is a monotypic evergreen shrub that is today endemic to the Channel Islands off coastal California. Based on its fossil record it is clear that this genus had a broader distribution in the Neogene than today, extending from Oregon to southern California and into west central Nevada (Erwin and Schorn 2000). The genus is first recognized in the Early Miocene (23 my) Collawash flora of Oregon and occurs in numerous Middle and Late Miocene localities, and, like today, is known only from far western North America.

The Neogene fruit and seed record of Europe contains many rosaceous genera (Reid and Reid 1915; Chandler 1962, 1963; Dorofeev 1963; Mai and Walther 1978; Martinetto 2001; Kvaček and Walther 1998, 2001, 2004). Reviews of older rosaceous fruit and seed literature can be found in Kirchheimer (1973); more recent reviews are in Mai and Walter (1978) and Mai (1995). *Prunus* endocarps are well known and have been reviewed by Mai (1984). By the Miocene, genera such as *Rosa*, *Crataegus* and *Rubus* are common elements of the Bohemian Bilini leaf flora (Kvaček et al. 2004). The Miocene-Pliocene of Saugbagger flora of Alsace, eastern France contains fruits of *Rubus*, *Crataegus*, *Mesopilus*, *Sorbus*, and *Prunus* (seven species; Geissert et al. 1990). In the Pliocene of the Netherlands Rosaceae were abundant, especially *Prunus*, which was repre-

sented by nine species (Reid and Reid 1915). *Rubus*, which is known as early as the Eocene (Chandler 1962, 1963) undergoes further radiation and has been documented in many European floras (summarized in Mai 1995). Other genera known in the European Neogene include *Cotoneaster* Medikus., *Pyrus*, *Mespilus* L., *Pyracantha*, *Stephanandra* Sieb. & Zucc., *Physocarpus*, *Comarun* L., *Potentilla* L., *Agri- monia* L., and *Filipendula* Mill. (Kirchheimer 1973; Mai 1984, 1995 and references cited therein).

In Africa Bruce Tiffney has recognized the first documented occurrence of a *Prunus* endocarp (subgenus *Amygdalus*) from the Neogene of Kenya (Tiffney, personal communication, 2005). In Asia *Prunus*, *Sorbus*, and *Rosa* are known from the Neogene of Japan (Tanai and Onoe 1961, Miki and Kokowa 1962, Tanai and Suzuki 1963). Rosaceous genera in Late Tertiary and younger strata (early Miocene to Early Quaternary) of Arctic and subarctic North America include *Dryas* L., *Crataegus*, *Fragaria* L., *Physocarpus*, *Potentilla* (four species), *Prunus* (two species), *Rubus* (two species), *Rosa*, *Sorbus*, and *Geum* L. (Matthewes and Ovendon 1990).

Pollen records of Rosaceae were reviewed by Muller (1981). He recognizes *Parastemon* A. DC type pollen in the Oligocene and lower Miocene of Cameroon and the upper Miocene of Borneo and *Filipendula* type and *Sanguisorba officinalis* L. from the Pliocene of the Netherlands. Pollen of *Adenostoma* Hook & Arn. (Chamise), an extant component of today's chaparral vegetation of California, has been described from the Late Pleistocene of the Santa Barbara Basin (Heusser 1978), and the Late Pleistocene La Brea Tar Pits (Stock 1992). Rosaceous pollen in the postglacial record of western Canada, has been studied by Williams and Hebda (1991).

Summary

Currently, the fossil record of the Rosaceae can provide some insights to dating the origin and evolution of major tribes and

genera within the family. Reciprocally, molecular data provides a context for interpreting what vegetative, fruit and floral characters are stable enough to be used in unraveling the array of fossil leaves that clearly have affinities within the Rosaceae.

In the fossil record, plant remains are typically found as disarticulated organs rather than whole plants. It is even more important in this type of situation to be able to recognize the salient features that define a given taxon. Rosaceous fruits and flowers are readily identifiable by their characteristic features, and indeed, fruit characters are the primary features of each traditional subfamily. Some rosaceous leaves also have distinctive characters, as do pollen grains and woods. It is possible to identify fossils to the family, and to a genus or subgeneric level when the right characters are preserved. Fortunately, the fossil record favors preservation of leaves, fruits and seeds and has the potential to provide insights to character evolution within the family.

It is often difficult to determine the phylogenetic relationships of these fossil occurrences to modern genera. Fossils with rosaceous affinities sometimes demonstrate a mosaic of characters of several extant taxa and are difficult to place systematically. Other rosaceous fossils lack sufficient diagnostic characters to place in extant genera, while still others show a wider range of variability than that found within individual genera today. Some of these larger groups may represent fossil evidence of polyploid or hybrid complexes, such as occur in the Rosaceae today. Because of these problems, paleobotanists have often been reluctant to assign some fossils to established genera (see Becker 1963). As a result the fossil record, particularly of the Paleogene has not been readily accessible to neontologists interested in rosaceous phylogeny. Neogene occurrences, particularly of fruits and seeds, are better known in Europe, however these too have not been exhaustively studied. While we readily acknowledge that there are limitations to what can be learned from the fossil record, we also recognize its unique potential as direct

evidence of the evolutionary history of rosaceous plant occurrence.

Biogeographical relationships within Rosaceae can also be illuminated partly with the fossil record. For example, a recently described fossil species of *Neviusia* from One Mile Creek has helped to interpret the disjunct relationship of *N. alabamensis* and *N. cliftonii* (DeVore et al. 2004). Other members of the rose family, for example, *Photinia*, which is documented in both Republic and Princeton floras, is only naturally distributed in Sumatra, Japan, and the Himalayan Mountains today (Wolfe and Wehr 1987). Fossil rosaceous taxa from western North America may also give clues to the genera with South American ties. For example, *Hesperomeles*, found at Republic, is currently distributed in Central America and Peru (Wehr and Hopkins 1994). However, the use of fossil taxa in discerning biogeographic patterns within the family will have to wait until additional taxa are formally described and affinities of these fossil members of Rosaceae can be assessed.

The family clearly radiated in response to the active tectonic margin of western North America, generating directly, or indirectly, new habitats as suggested by Stebbins. European occurrences are widely documented, especially for the Neogene, and additional Asian, and rare African representatives are known. As current studies on different continents progress, it will soon be essential to examine the global distribution of the family to better understand the details of its complex evolutionary history and paleobiogeography.

This review is dedicated to the late Wes Wehr, Burke Museum of Natural History & Culture, Seattle, who inspired and encouraged our interest in the fossil Rosaceae, and the late Jack A. Wolfe, who made many of the original identifications of Republic Rosaceae and recognized the paleoecological significance of leaf physiognomy. We thank Drs. Volker Wissemann and C. S. Campbell for inviting our participation in this symposium volume; Wes Wehr and Ron Eng, Burke Museum of Natural History & Culture, Thomas and Richard M Dillhoff, Evolving Earth

Foundation, and Lisa Barksdale and Catherine Brown, Stonerose Interpretive Center for access to fossils for study; Steven R. Manchester for photographs of fossil *Spiraea*-like fruits and extant *Spiraea*; Bruce Tiffney for literature and helpful comments on a draft of the manuscript; Harald Walther and an anonymous reviewer for helpful comments on the manuscript; Gary Lundell, University of Washington Libraries, for library assistance; John C. Benedict for technical assistance; and the late G. Ledyard Stebbins, Jr. for his insights on the significance of the fossil record to rosaceous evolution. This research was supported in part by National Science Foundation grants EAR-0345569 (to MLD) and EAR-0345838 (to KBP).

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