**Canadian Journal of Earth Sciences**
Revue canadienne des sciences de la Terre

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**Biotic processes in the Okanagan Highlands floras:  possible evidence of hybridization in plants adapting to a temperate forest**

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1

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**Abstract**      Hybridization is a key mechanism for increased diversification and speciation among modern plants, and is especially important in certain families such as Rosaceae and Anacardiaceae. This mechanism is found to occur most commonly in areas of ecological disturbance, distribution and migration. Resulting hybrid individuals have characteristic intermediate or mosaic patterns that combine those of the two parents in morphologically distinct and identifiable ways. The diverse latest early Eocene flora of Republic, Washington, USA is among the most collected of the Okanagan Highlands floras. This fossil flora includes relatives of modern taxa that are known to hybridize and produce characteristic patterns of leaf morphology and venation (Rosaceae; Anacardiaceae). In this study we document patterns found in representative fossil leaves that are comparable to those indicative of hybridization in the modern relatives. We use the genera *Sorbus* L. (Rosaceae) and *Rhus* L. (Anacardiaceae) as models to demonstrate potential hybridization in the latest early Eocene.

Key words:  Hybridization; leaf morphology, plant evolution, Rosaceae, Rhus

**Introduction**

The first records of forests with a significant proportion of temperate taxa in North America occur within the latest early Eocene Okanagan Highlands floras of British Columbia,

Canada and eastern Washington, USA (Johnson 1996; Wing and DiMichele 1996; Greenwood et al. this issue). During a time when coeval coastal floras were dominated by taxa indicative of continuous high temperatures and abundant rainfall ("megathermal" conditions, e. g., Breedlovestout et al. 2013) the higher elevation Okanagan floras document the radiation of several important present day temperate groups such as Betulaceae (Crane and Stockey 1986; Pigg et al. 2003), Rosaceae (Wehr and Hopkins 1994; DeVore et al. 2004; DeVore and Pigg 2007; Benedict et al. 2011), Pinaceae (Schorn and Wehr 1996) and Sapindaceae (Wolfe and Tanai 1987; McClain and Manchester 2001; Wang et al. 2013), among others (Wolfe and Wehr 1987, 1991). As such, they have the potential to provide some insights regarding the acquisition of traits present in dominant species that today define the character of Northern Hemisphere deciduous forests.

Understanding the dispersal and radiation of plants into new habitats, whether they are high altitude, or high latitude depends on our ability to recognize the occurrence of certain anatomical and morphological features in the fossil record. Previously, we documented the presence of heteromorphic growth of *Zizyphoides* Seward and Conway leaves at the Republic, WA site, as evidenced by their long-shoot and short-shoot morphological differences (DeVore and Pigg 2013). Fossil leaves that have been difficult to delineate systematically appear to compare closely to extant dimorphic leaves such as those known to occur in *Populus* L. (Salicaceae, Eckenwalder 1980), and the Asian genus *Cercidiphyllum* Sieb & Zucc. (Cercidiphyllaceae, Krassilov 2010). Plants with long shoot/short shoot branching have preformed leaves that overwinter in the buds on short shoots and become immediately available for photosynthesis upon bud break, while long shoot leaves later fill out the canopy (DeVore and

3

Pigg 2013). This type of heterophylly is apparently a mechanism that maximizes the opportunity for photosynthesis early in the spring in plants with certain types of dormancy.

In a similar manner, diverse and distinct patterns of leaf morphology seen in radiating hybrid and polyploid complexes in modern Rosaceae, and Anacardiaceae are recognizable in the fossil floras of the Okanagan Highlands, particularly at the well collected sites of Republic, Washington. In fact, researchers working on the leaves at Republic noticed early on that there were complexes of leaves with unusual morphologies that were difficult to study systematically (e.g., Manchester 1999).

` In this paper we explore the variability seen in these leaves with unusual morphologies that show features characteristic of hybrids. In particular, we document leaves resembling *Sorbus* L. and others assignable to *Rhus* L. that show a range of morphologies consistent with those of modern hybrids in these genera. We show that both changes in leaf shape, particularly transitions between entire and pinnately compound leaf morphology, and distinctive venation patterns that are known in modern hybrid complexes occur among large collections of compressed fossil leaves from Republic. Using modern examples of *Sorbus* and *Rhus* as models, we explore the possibility that hybridization was an important process in the latest early Eocene as it is in disturbed habitats and newly opened habitats today.

## Material and methods

Fossils are described from lacustrine shales that occur at sites in and around the town of Republic (Ferry County) eastern Washington, USA (Gaylord et al. 2001). The fossils are found in the Tom Thumb Member of the Klondike Mountain Formation and dated latest early Eocene (Archibald et al. 2011; Greenwood, et al. this issue). Specimens were photographed with a digital

4

camera and modified slightly in Adobe Photoshop with standard tools to increase contrast (Image: adjustment: levels), lighten critical areas in shadows (Dodge), align photos exactly with one another (Image: rotation: arbitrary), and remove minor imperfections (Eraser, Clone stamp tool). The specimens are housed at the Stonerose Interpretive Center, Republic, Washington.

*Protocol*

To investigate hybridization among fossil leaves from Republic we propose establishing a protocol for evaluating sets of variable leaf types. The components of this model are as follows: 1) There must be a morphological set of features that are homologous to both the extant and fossil taxa; 2) It is necessary to demonstrate that the morphological character is not linked with other phenomena such as long shoot-short shoot relationships or sucker shoots; 3) The proposed fossil hybrid must be assignable to an extant taxon; and 4) There must be a region where the extant taxon linked with the fossil taxon are actively forming a hybrid complex.

In order to test this hypothesis of hybridization in Republic plants we chose the genus *Sorbus* (Rowan), a member of the Rosaceae. This genus was selected as a model since its leaf architecture is well known as a result of a detailed analysis of modern taxa with hybrids (Merrill 1978). We applied our criteria described above to a collection of more than 90 maloid Republic leaves representing a complex of taxa with potential affinities to *Sorbus*.

As a proof of concept, we wanted to test our protocols on another taxon. We examined 85 fossil *Rhus* leaves from the collection housed at Stonerose Interpretive Center, Republic, Washington. *Rhus* also has pinnately compound leaves and hybrids have a tendency to have variant leaf morphology, in some cases, fusion of the upper three leaflets.

**Results**

Sorbus-like leaves from Republic each show the unusual gradational compound-to-pinnate- to-entire leaf morphology found in modern hybrid Sorbus (Fig. 1A-F ). Figure 1A shows the modern species Sorbus aucuparia L. ("Scottish Rowan") from the Glencoe, Scotland area (Nelson-Jones et al. 2002; Chester et al. 2007; Pellicer et al. 2012; Ludwig et al. 2013). Figure 1E is from the hybrid variety Sorbus x thringiaca (Ilse) Fritsch. Like modern hybrid Sorbus species, in the fossils (Fig. 1C, D), there is an apparent cross between a pinnate parental species (Fig. 1B) and an entire-leafed form (Fig. 1F). As is the case with modern Sorbus, these fossil forms show the classic pattern of complex morphological variation where several taxa hybridize and continue to backcross with one another (introgression).

Leaves also show a classic pattern of venation disorganization as described by Merrill (1978) for modern hybrid forms (Fig. 2A-F). In particular, the termination of veins at the margin is highly irregular. Using Merrill's (1978) terminology (lower, compound leafed portion = rachis; upper apical blade = primary vein), the apical blade has simple, craspedodromous venation (Fig. 2A, B). At the base of the apical blade there are often intersecondaries. In some cases, the intersecondaries may divide and branch beneath the sinus and from a characteristic bracing vein pair around the sinus (Fig. 2A, B). In other cases intersecondaries share a point of origin with a secondary vein, a pattern of intersecondaries that also occurs in leaflets of extant Sorbus aucuparia in leaves produced by sucker shoots.

Another phenomenon seen in extant Sorbus leaves is a difference between leaves in the crown of the plant and those produced by the plant's sucker shoots (Fig. 3A, B). Leaves borne by sucker shoots are notably larger than crown leaves, in this case around 7.5% so. Sucker shoots in

6

*S. aucuparia* for example, are pinnafid, that is mostly fused toward the apex but only slightly so (Fig. 3A). In contrast to the crown leaves which bear only small, unpronounced teeth (Fig. 3B), sucker shoot leaves have highly serrate margins (Fig. 3A). Sucker shoots, in contrast to the hybrid leaves described above, have regular, and not disorganized venation.  We recognize fossil *Sorbus*-like leaves with a similar morphology to these modern sucker shoots (Fig. 3C-E).

We also looked at leaves of *Rhus* that show a range of variation (Fig. 4A-G). Here we find mainly pinnately-leafed species, however, they have an unusual degree of fusion towards the top portion of the leaves on some specimens (Fig. 4B, D). Figure 4B shows a compound leaf with upper leaflets that are fused and approaching a trifoliate morphology, whereas Fig. 4F shows two fused leaflets.  Also notable on this specimen is the amount of vein disruption which provides additional support for a hybrid origin (Fig. 4B, compare veins in leaflets on right and left sides).  In this light, it is possible that trifoliate forms found within *Rhus* are the result of ancient hybridization.  General leaflet morphology and degree of marginal serration may also vary within a single specimen (Fig. 4F, G).

## Discussion

### The presence of features associated with hybridization in fossil leaves from Republic

*Sorbus*

In order to consider the possibility that leaves with unusual morphologies at Republic might be hybrids, we chose two readily identifiable genera known to hybridize today. *Sorbus sensu lato* is one of two distinct species groups that contain members with pinnately compound leaves within the traditional subfamily of Rosaceae Maloideae (Robertson et al. 1992).  The *Sorbus* complex has deciduous leaves with serrate (or rarely) entire margins. Within Maloideae

the only genus outside of the *Sorbus* complex that has pinnate leaves is *Osteomeles* Lindl. In contrast, to *Sorbus*, *Osteomeles* is characterized exclusively by evergreen, entire margined leaves.

*Sorbus* parental diploids have either entire or pinnate leaves and crosses of species with differing leaf morphologies produce hybrid offspring with intermediate leaf forms. Commonly, leaves of hybrids have pinnate leaflets towards the base intergrading into an entirely laminate region toward the apex (Merrill 1978). In his study of hybrids in extant forms of *Sorbus*, Merrill (1978) recognized six stable higher order venation and marginal characters and applied Hickey's venation ranking system (Hickey 1971, 1977) to assess regularity of leaf organization. Merrill also looked at the overall morphology of the leaves themselves.

We see patterns similar to those of extant hybrid *Sorbus* leaves (Nelson-Jones et al. 2002; Chester et al. 2007; Pellicer et al. 2012; Ludwig et al. 2013) in the Republic *Sorbus*-like specimens, both in terms of a gradational compound-to-pinnate-to-entire leaf morphology, and in the types of vein disorganization described by Merrill (1974). Based on these similarities we conclude that there is good evidence for hybridization within the Republic *Sorbus*-like complex. Further detailed analysis and its systematic implications will be explored further in another contribution.

Another distinct morphology that occurs in *Sorbus* is that of its sucker shoots (Fig. 3A-D). Unlike hybrid leaves, leaflets of plants produced by sucker shoots have regular, rather than disrupted venation. However, sometimes sucker shoot leaves show a degree of fusion of the terminal leaflets (Fig 3). We can recognize sucker shoot leaves of *Sorbus*-like plants in the fossil record by these traits (Fig. 3 ).

This surculose, or sucker-producing habit, in *Sorbus* and other maloid genera, is frequently paired with the reproductive mode of agamospermy, or the production of fruits without sexual reproduction (Robertson 1992). The combination of these vegetative and reproductive mechanisms provides some stability of maintaining the great range of genetic novelty in introgressive taxa. Agamospermy, and the production of suckers, along with the generation of shoots from a bud at the base of a trunk or via adventitious root buds enables the expansion of a novel, adapted form, rapidly into a new, favorable, habitat.

What is interesting with some of these maloid taxa, like *Sorbus*, is that the sucker shoots have distinct, toothed leaves. The ability of sucker leaves to be more efficient photosynthesizers, is an avenue worth exploring in future work. A sucker, being much smaller than the parental shoot, would have to compete with a parent. The presence, and the ability of sucker shoots, with their definitively toothed leaves, could provide a more efficient leaf form for photosynthesis than those produced by the parental plant (e.g., Royer and Wilf 2006).

*Rhus*

The second genus we considered was *Rhus*. *Rhus integrifolia* (Nutt.) W.H. Brewer & S. Watson and *R. ovata* S. Watson are unusual species within the genus since they have entire leaves as opposed to trifoliate or pinnate ones. Both species are part of a hybrid complex in Arizona, California, and Nevada. Young (1974a, b) completed a morphological treatment of this group and found that some putative hybrids had irregularly trifoliate leaves and interpreted this condition as reflecting ancestral relationships with a pinnate-leaved species within the genus.

The fossil form *Rhus malloryi* Wolfe and Wehr, was described in their monographic treatment of the Republic flora on the basis of a small number of specimens (Wolfe and Wehr

9

1987). In contrast, today we have a much larger sample. Thousands of specimens have been

collected over the past 30 years by the public collecting at the Republic sites under the auspices

of the Stonerose Interpretive Center (Perry and Barksdale 1996; Greenwood et al., this volume).

As a result, the wide array of *Rhus* specimens available to us clearly represent multiple species,

many appearing to having morphologies suggestive of hybrid forms.

The Republic flora was in an active, tectonic region of western North America and the

complexity of habitats would have been the ideal situation for not just hybridization, but also

agamospermy (producing seeds without fertilization) and vegetative reproduction via suckering.

In regards to subfamily Maloideae, Robertson et al. (1991, 1992) proposed lineages the model of

polychotomous model of alloploid gene pool evolution within subfamily Maloideae, in which

continuing crossing and backcrossing through geologic time produces separate subfamilies

(Potter et al. 2007).

Comparing distribution patterns of modern *Sorbus* and other related taxa in regions where

they are actively hybridizing and reproducing agamospermously, provides evidence of a biotic

mechanism for taxa dispersing not as single entities, but as linked sets of species.  This changes

the way we model the response of some plant groups to climate change and other anthropogenic

factors.  The scope of the present contribution is one of proof of concept. We offer it with the

intention that plant paleobiologists can apply this approach to documenting the patterns of leaf

anatomy and morphology in other plant groups. Although we have no way to definitively

identify a hybrid without direct genetic evidence, the patterns elucidated in this paper provide

some degree of indication that patterns, seen today in extant hybrids, could potentially indicate

the presence of hybrids in the past.

*Hybridization in the evolution of Northern Hemisphere temperate forests*

Okanagan Highlands floras provide a glimpse of the key genera destined to become dominant taxa within modern deciduous forests in the Northern Hemisphere. An important question to address is: How may hybridization have contributed to the development of deciduous plant communities in the Northern Hemisphere?

Axelrod (1966) hypothesized that the development of the deciduous habit was a means by which hardwoods of warm temperate to tropical climates could invade a new adaptive zone and suggested this mechanism may have been the driving force behind the colonization of higher latitudes. Species which have invaded higher elevations, as well as latitudes, in the Northern Hemisphere appear to be capable in flexibly, quickly responding to changes in summer and annual temperatures (Pauli et al. 1999; Walther et al. 2005; Cannon et al. 2007).

Many of these adaptations involve complex responses that demonstrate the ability to have a range of different means of a collection of buds having different fates. Some buds overwinter in an advanced state of development (Eckenwalder 1980; DeVore and Pigg 2013); others abort, still others differentiate into pistillate and staminate catkins (Ishihara and Kikuzawa 2004). Combined with these differing fates of buds on the same tree is dormancy during periods of unfavorable growth. All of these various fates are triggered, at least to some degree, by an environmental signal linked with seasonality. Although growth form is an obvious means of pinpointing such a change, the ability to respond in such a manner also has to be linked with the plants' evolutionary mechanisms. Traditionally, the two evolutionary processes often invoked to explain radiations of plants are hybridization and polyploidy (Stebbins 1966; Grant 1981).

In the Okanagan Highlands, the family best known for using these evolutionary mechanisms is the Rosaceae. Thus, the presence of diverse fossil Rosaceae in the Okanagan

11

Highlands attracted the attention of the plant evolutionary biologist G. Ledyard Stebbins (DeVore and Pigg 2007). However, although Stebbins contributed an extraordinary body of work on the chromosomal evolution of plants and hybridization, his numerous projects never enabled him to pursue integrating the fossil record into his concepts of plant speciation. At the time of his interest in the issue in the early 1990s, (DeVore and Pigg 2007), the number of fossil specimens of rosaceous taxa needed to uncover patterns of hybridization did not yet exist. Today they do exist and we can start to elucidate putative hybrids in the fossil record.

It is interesting to compare the pattern seen in temperate forests of the Northern Hemisphere with their Southern Hemisphere counterparts. They differ markedly from one another today, as a result of the influence of separate and distinct geohistorical factors. No doubt, an underlying influence for these hemisphere-wide distribution of characters is related to continental configuration and its subsequent influence on climate. In the case of the Northern Hemisphere, Asia, Europe and North America formed a "ring" around the Arctic Ocean. During the Mesozoic and Cenozoic various connections existed among these continents (e.g., the North Atlantic Land Bridge; Tiffney 1985; Tiffney and Manchester 2001). Deciduous forests are found on all the northern continents and reflect a history that was strongly influenced by dispersal. In contrast, temperate forests of South America have been impacted more strongly by continental variance. It may be that hybridization thus played a more significant role in the evolutionary history of the Northern, in contrast to the Southern Hemisphere temperate floras.

## Conclusions

The fossil record can provide some useful clues to evolutionary processes in plants despite the fact that we cannot count chromosomes directly from a fossil or turn to molecular

biology to trace the ancestor of hybrid species. What <u>can</u> be documented is the recognition of morphological patterns in the fossil record, that are congruent with those seen in these same families that today are well known to produce these patterns as a result of their biological processes. This approach to understanding mechanisms in deep time, has been underexploited in the past, with only a few rare cases where hybridization has been invoked. Examples include crinoids (Ausich and Meyer 1994), snails (Goodfriend and Gould 1996) and corals (Budd and Pandolfi 2004).

Plant biologists for years have recognized that hybridization, defined as the crossing of individuals of different species, and introgression, the process of transferring genes between species via backcrossing, have permitted genetic novelties to accumulate in the blink of an eye in comparison to a longer, gradualistic process of accumulated mutations (Anderson and Hubricht 1938; Anderson 1949; Stebbins 1966; Grant 1981; Twyford and Ennos 2012). These processes have been well documented among extant groups, and are readily accepted into the understanding of how plants diversify today. In fact, they are even given a special nomenclature that indicates hybrids as products of genetic crosses between different parental species. The taxonomic efforts of paleobotanists have been devoted largely to identifying the affinities of fossils in relation to extant plants and to other fossil forms, generally at a larger scale. The presence of intermediate, difficult-to-identify morphologies has been regarded more as a taxonomic nightmare than as an opportunity to understand the mechanisms that produce these patterns. Some questions can only be addressed with large samples that reflect the range of variation present, and we now have the large collections of leaves from Republic that provide the opportunity to address the role of such mechanisms as hybridization.

In using the fossil record to trace the dispersal of taxa we model, we tend to think of their

13

existence as isolated units (e.g., species) with individual distributional histories.  In the case of

*Sorbus*, agamospermy, hybridization, and polyploidy generate a species complex as the dispersal

unit as opposed to single, definable, distinct species.  In this light, the concept of how we

determine taxonomic units and model their dispersal in deep time needs to be considered

carefully.  Histories of species may be linked by speciation mechanisms, and these combinations

of species mechanisms provide a range of variation necessary to invade new habitats.  Mallet

(2005) referred to the vigorous amount of gene flow between species where their distributions

overlap permitting introgression as the "invasion of the genome".  If this process occurred in the

Republic flora with *Sorbus*-like ancestors, then where do we find blurred speciation boundaries

and introgression presently occurring?

Today European species of *Sorbus* have greatest diversity in the Czech Republic,

Hungary, Great Britain and Germany (Phipps et al. 1990; Aldasoro et al. 1998; Bednorz 2006).

Mainly a temperate genus, there is a second center of diversity in Asia, but it has not been the

focus of biosystematics. Outliers of the genus' primary distribution include Malesia, and species

in Greenland and Siberia (Aldasoro et al. 1998).  It has been proposed that *Sorbus* originated in

East Asia, and species migrated to Europe and North America from this region (Gabrielian 1978;

Jankun 1993; Aldasoro et al. 1998).  In both cases, there is a pattern of having at least one

widespread member (e.g., in the United Kingdom it is *Sorbus aucuparia*) which is linked with a

suite of species via hybridization.  This represents an active evolving center for the genus. The

complex as a whole may invade high elevations and other regions where there is heterogeneity in

its range. These kinds of species complexes also would have the potential to generate a new,

more fit, widespread species when selected for by major changes in climate.

This does not mean we are recognizing today's hybrid complexes in the Eocene, since

many generations of plants have existed since then. It is however, demonstrating that hybridization as a mechanism that produces a recognizable footprint today can be seen in the array of morphologies we see in the Republic flora. This is the case in several notable families, such as Rosaceae and Anacardiaceae, where hybridization is still a major process today.

## Asymmetrical characters and applications for future studies

All of the characters we describe for putative hybrid leaves of Anacardiaceae and Rosaceae are ones demonstrating asymmetry, whether at the level of asymmetric laminar division of compound leaves or within patterns of leaf venation. Both of these kinds of asymmetrical characters show developmental instability, and have been documented clearly as being linked to hybridization in extant, woody genera (e.g. Hochwender and Fritz, 1999; Wilsey et al., 1998).

This recognition suggests that if we wish to document the occurrence of hybridization in the fossil record, instead of looking for additive features leaves from a contemporaneously deposited layer, we should focus on asymmetrical characters that represent non-random, non-directional deviations from symmetry, a phenomenon known as fluctuating asymmetry (FA). FA has been linked with both environmental stress and genetic irregularities. On the one hand, environmental stresses associated with both high elevation and hybridization have been implicated (Wilsey et al. 1998). On the other, Hochwender and Fritz (1999) attribute FA in *Salix* to the disruption of coadapted gene complexes by hybridization.

When applied to fossil leaf specimens, an index of FA would provide a new means for elucidating hybridization in the fossil record. In particular, it would give us a foundation for developing our own means of quantifying FA for *Betula* and other woody taxa where the extant

15

pattern is known and we have the number of specimens needed for statistical treatment.

## Acknowledgements

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19

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**Figure captions**

Figure 1. Two extant *Sorbus* species, compared with fossil leaves. (A) Extant *Sorbus aucuparia* L. ("Scottish Rowan") from the Glencoe, Scotland area. Note pinnately compound leaf with 3 terminal leaflets. (B) Fossil leaf, pinnately compound with 3 terminal leaflets like that of extant specimen.  Compare with Fig. 1A. SR 02-09-01, collected by Staff 2002. (C) Fossil of mostly entire leaf with 2 basal pinnae, and transition from pinnafid to entire leaf. Note the pair of basal leaflets. SR 10-74-21AB, collected by Travis Wellman. (D) Fossil of mostly entire leaf with 2 basal pinnae, and transition from pinnafid to entire. SR 91-05-07, collected by Erma Henry. (E) Extant *Sorbus* x *thringiaca* (Ilse) Fritsch leaf, showing intermediate morphology with a transition from pinnate to lobed to entire foliar morphologies. Note distinct pinnate leaflets at base of leaf. (F) Fossil, entire leaf with serrated margins. SR 92-06-04, collected by Marty Daniels. Scale bar: Fig. 1B-D, F = 5 cm.

Figure 2. Fossil *Sorbus*-like leaf showing disrupted venation patterns. (A) Overview of part

specimen to show general appearance. Note secondaries that continue into marginal teeth and

intersecondaries that may branch or enter sinus. (B) Counterpart of 2A, inverted horizontally, to

show detail of venation. (C) Higher magnification of Fig. 2B to show detail of disorganized

appearing higher venation. (D) Detail of basal part of leaf in Fig. 1D, showing detail of venation

in separate leaflets. Fig. 2A-C, SR 00-12-03. Collected by Stephen Bangs. Fig. 2D. SR 91-05-07,

collected by Erma Henry).  Scale bar: Fig. 2A-B = 2 cm, C-D = 0.5 cm.


Figure 3.  *Sorbus aucuparia,* leaf from sucker shoot to compare with leaf from crown, and fossil

*Sorbus*-like leaf with similar morphology as sucker shoot leaf. (A) Pinnately compound leaf from

sucker shoot of extant *Sorbus aucuparia* showing leaflets with highly serrate margins. Entire leaf

is 20.3 cm long (B) Pinnately compound leaf from parent plant of *Sorbus aucuparia.* Note less

pronounced marginal serration. Entire leaf is 12.7 cm long. (C) Individual fossil leaflet like those

of extant *Sorbus* sucker shoot, showing double serrations. SR 06-66-01A, collected by David,

Deborah & Sterling Morgan. (D, E). Detail of Fig. 3C showing regular venation and distinct

marginal teeth. Figure 3D is more distal, 3E more proximal portion of same leaf. Scale bar: Fig.

3A, B= 1 cm, C= 0.5 cm, D and E= 1 mm.



Figure 4. Fossil *Rhus* leaf showing fusion of terminal leaflets and disrupted venation.

(A) Pinnately compound leaf. Note variation in leaflet morphology. SR 91-01-13, collected by

Stephanie Dinkins. (B) Specimen showing three-lobed apex. Note differences in venation on left

and right side of leaf. SR 00-05-19, collected by Howard Ramey. (C) Pinnate leaf with more

uniform leaflet morphology and two terminal leaflets. SR 97-05-12, collected by Alison Leach.

(D) Three-lobed terminal leaflet. SR 07-39-11, collected by Patty Jo Austin. (E) Three-lobed

leaf.  SR 95-03-29, collected by Per Igerson and Wes Wehr. (F) Leaf with two-lobed apex. SR

02-18-11, collected by Brian Hutchinson. (G) Pinnate leaf with lobed entire apical leaflet. Note

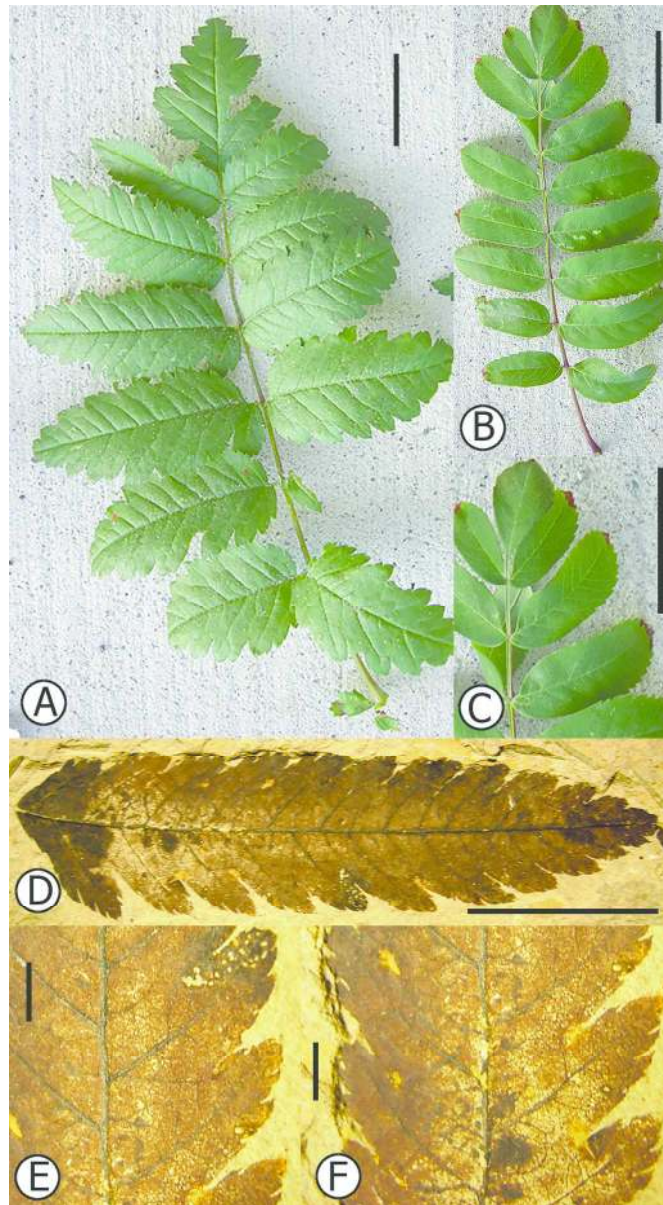pinnate organization SR 95-25-11, collected by Jonathan M. Wittry II. Scale bar: = 2 cm.
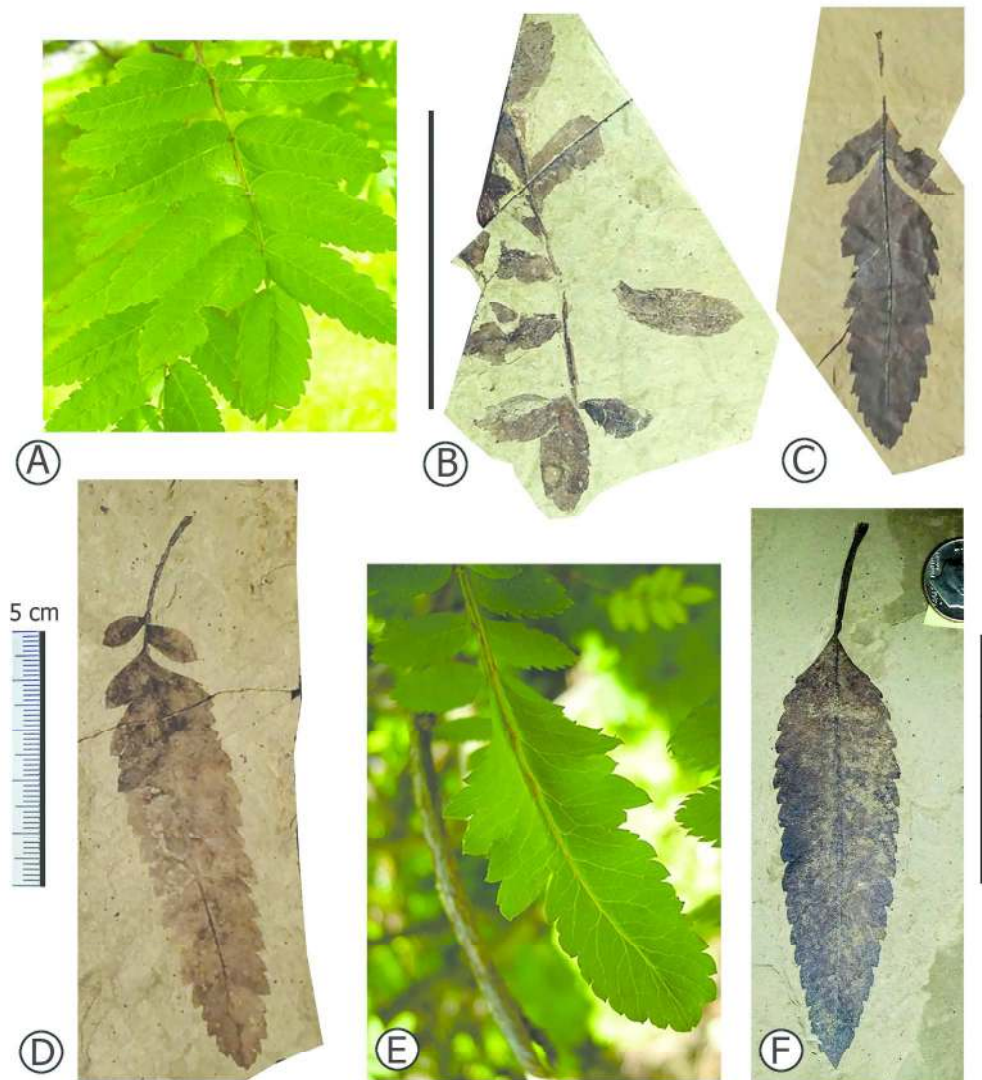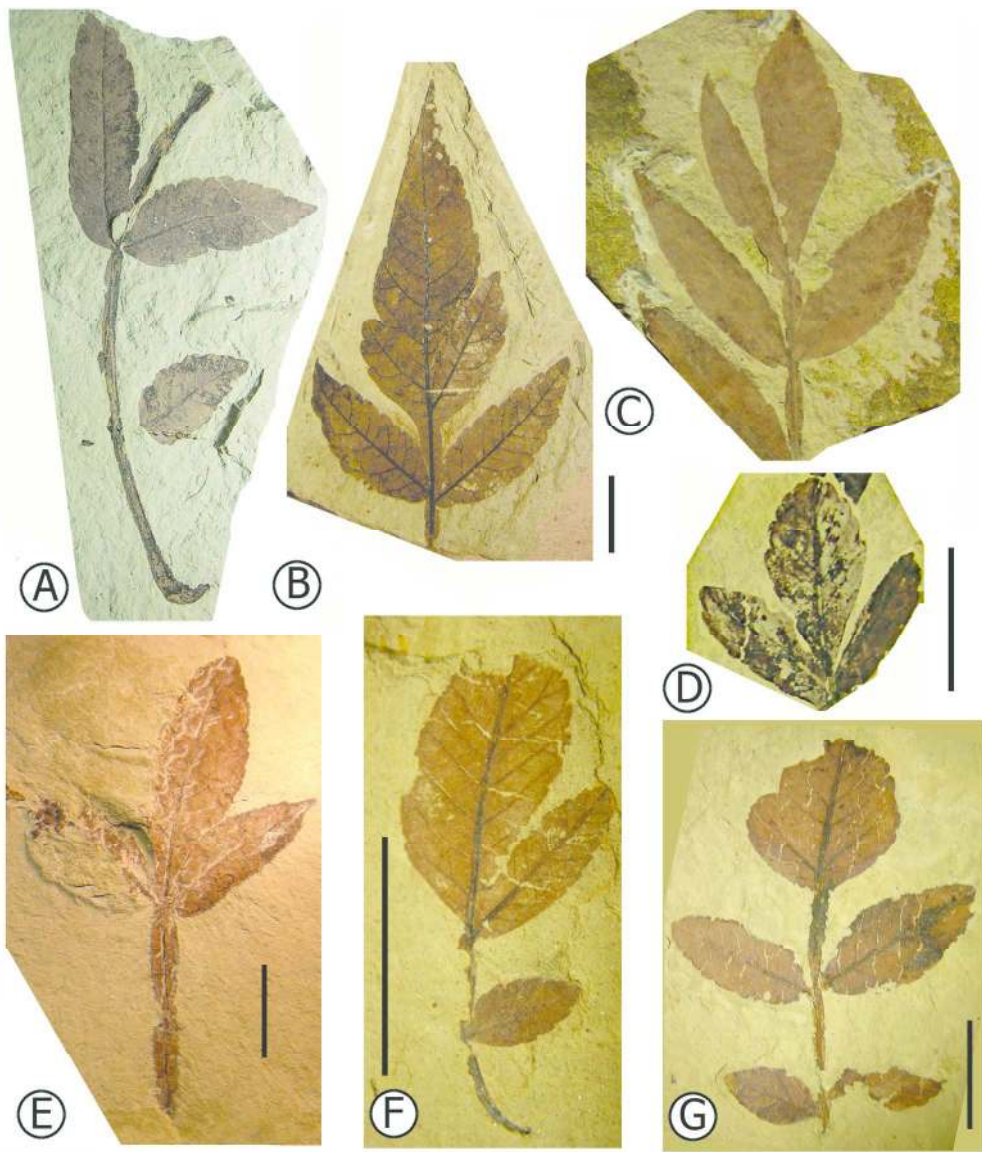
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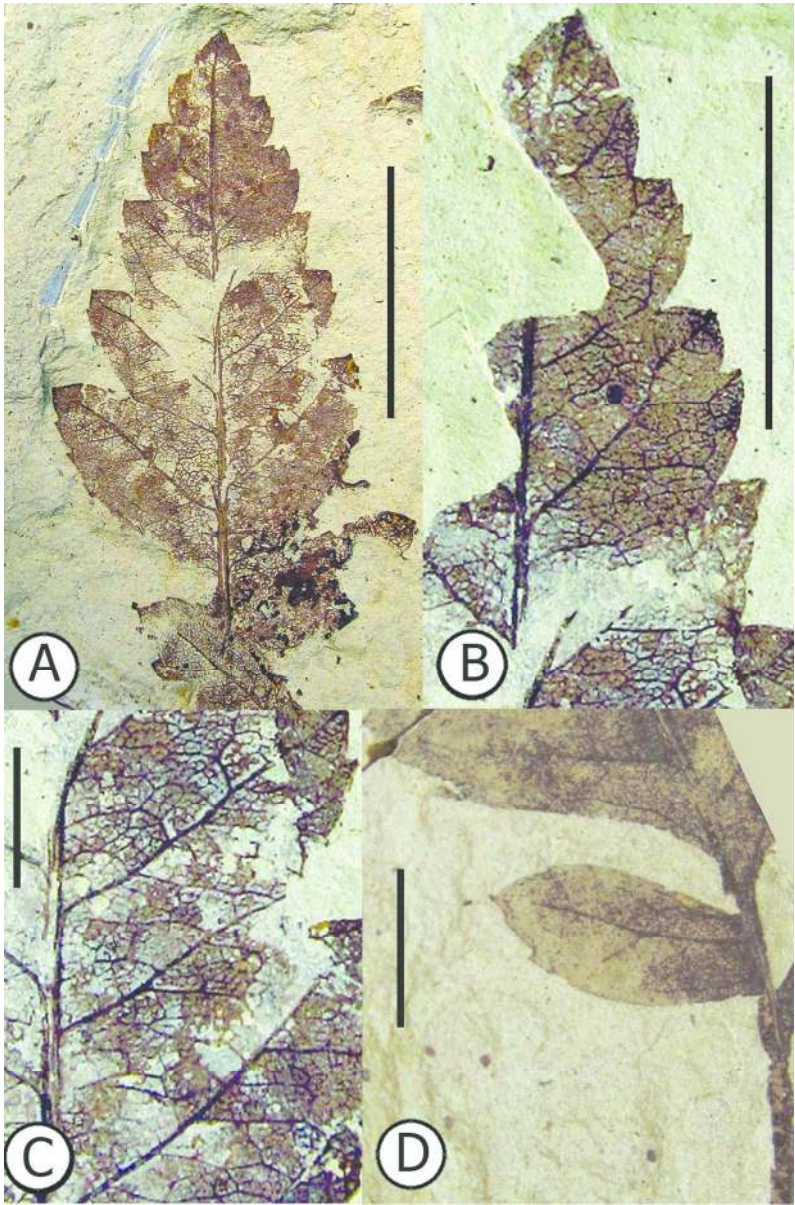
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