ANATOMICAL VARIATION IN THE WOOD OF ROBINIA PSEUDOACACIA L.
AND THE IDENTITY OF MIocene FOSSIL WOODS FROM
SOUTHWESTERN UNITED STATES

by

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Summary

A detailed analysis of selected quantitative features was made of secondary xylem from the trunk, branch, and root of a specimen of Robinia pseudoacacia L. The analysis serves as a basis for interpreting two suites of fossil woods closely similar to the wood of Robinia. One assemblage had its provenance in western Nevada and the other in southern California. Results of the survey show considerable overlap in ranges of variation in the fossils and extant woods. These findings parallel results of a similar investigation by Matten et al. (1977). Woods from both fossil localities fall within the specifications of the organ species Robinia zirkellii (Platen) Matten, Gastaldo & Lee. The survey also revealed the kinds of differences that may be found in species of Robinia growing in dissimilar habitats. Differences noted among trunk, branch and root wood of extant Robinia make it possible to distinguish these organs among the fossils. 

Key words: Robinia, fossil wood, Miocene, Nevada, California.

Introduction

Paleobotanists working with petrified wood are faced with several problems in attempts to determine the significance of differences between fossils exhibiting similar structural patterns. Although most workers are aware that quantitative characters vary throughout a given tree and within a population, for most species, either there are very few data on the extent of variation or adequate comparative material is lacking. Moreover, the paleobotanist often works with thin sections of a small portion of a fragment of a fossil and reference material of even smaller sections of modern woods, hence differences that appear significant may only be a matter of statistical error through inadequate sampling. In order to evaluate the differences between fossils of different ages, it is necessary to know how fossils compare with the range of differences found among and within modern species of the genus to which they have been assigned. With this in mind, a survey was made of the trunk, branch and root of a single tree of Robinia pseudoacacia L. The results not only demonstrate the extent and kinds of differences and the importance of adequate sampling, but also serve as a frame of reference for interpreting relationships of the fossils to each other and to their presumed counterparts.

Fossil leaves have provided an extensive body of information about the diverse vegetation of the Late Tertiary in southwestern United States and how alterations in its composition through time reflect cooling and increasing aridity (Axelrod 1958). Wood is also abundant in Tertiary rocks of the region but it has not been studied in detail. Such studies are of potential importance in paleoclimatology and paleofloristics. For example, wood may provide evidence that tests leaf identifications, and, to some extent, environmental conditions can be inferred from wood structure. Also, in some localities wood is the only source of data. This paper considers fossil wood of Robinia from two Miocene localities, Dove Spring, California, and Stewart Valley, Nevada. The Stewart Valley woods corroborate previously published leaf identifications, and because leaves were not preserved in the Dove Spring locality, the woods provide most of the information about the vegetation that supported a diverse mammalian fauna.
Geological setting

Stewart Valley, Nevada

Stewart Valley is a fault-bounded depression between the Cedar Mountains to the east and the Gabbs Valley Range to the west at lat. 38° 15' N and long. 117° 56' W and about 50 km. east of Hawthorne, Nevada. The following description of the stratigraphic position and location of the fossil locality is based on information in Schorn et al. (1989; also pers. comm.). Stratigraphically the 'petrified forest' horizon is correlated with the middle Miocene Barstovian stage of mammalian geochronology. Volcanic ash from a horizon just above and in conformity with a lateral equivalent of the wood horizon yielded a potassium/argon date of 15 million years ago (Ma). The geology of the region indicates a time of interrupted drainage and the formation of small lakes with subsequent, perhaps sudden changes resulting in a major flooding and creation of a very large lake. A consequence was the inundation of near-shore vegetation. Some of the trees still stand where they were drowned and are the source of the wood assemblage under investigation. Ultimately the lake became the repository of an extensive representation of the regional flora and fauna of the time.

Dove Spring, southern California

The Dove Spring Formation is exposed in the El Paso Basin in southern California which lies between the El Paso Mountains on the southeast and the Sierra Nevada on the west at lat. 35° 25' N. and long. 118° W. The fossil beds are exposed in Last Chance Gulch. When fossil woods of oak, palm, and black locust (Robinia) were first described by Webber (1933), the outcrop was considered to be a unit of the Ricardo Formation and Pliocene in age. However, it is now interpreted as a unit of the Dove Spring Formation, a new division of the former Ricardo Formation (now elevated to Group status; Loomis & Burbank 1988) and of Upper Miocene age. The fossils represent vegetation inundated by water-deposited volcanic ash, and some embedded tree stumps were still in upright position when samples studied by Webber were collected (David Whistler, pers. comm.). Whistler and Burbank (1992) have devised a magnetic polarity stratigraphy for the Dove Spring Formation that can be correlated with the magnetic time scale of Berggren et al. (1985). According to Whistler (pers. comm.), the wood horizon lies close to the 13 Ma level, possibly about 12.8 Ma. Webber's fossils would now be considered Upper Miocene and correlated with the Clarendonian stage of mammalian geochronology.

Materials and Methods

The tree of Robinia pseudoacacia examined had lived for over 80 years in a park in Palo Alto, California. Specimens derived from it are designated by the collection number VMP8900. The trunk was at least 70 cm in diameter and contained growth rings as wide as 15 mm and as narrow as 1 mm. The somewhat flattened branch was 7–9 cm in diameter with rings 1–5 mm in width. One root was 10 cm in diameter and another 2.5 cm. Widest growth rings in the former measured 7 mm and in the latter 2 mm. Since data were obtained from thin sections of the fossils, only sectioned material of the extant species was used. Blocks 1.5 cm on all sides were cut from: 1) two areas of the trunk, one from the interior and containing wide rings and the other from the exterior and containing narrow rings; 2) the upper (adaxial), lower (abaxial) and lateral portions of the branch; 3) from both root specimens. Sections were cut by hand, stained in toluidine blue and mounted 15 to 20 per slide. At least two different slides each were made from the radial, tangential and transverse sections. A minimum of 25 measurements was taken for each feature.

Because tissues in fossil woods are often distorted due to diagenic processes, pores may appear compressed, thus altering the ratio between tangential and radial diameters. In order to compensate for this distortion, the average diameter of each pore was estimated by adding the radial and tangential diameters and dividing by two. These measurements are designated RTA (radial tangential average). The RTA facilitates comparisons in that approximate pore size can be expressed with a single number.
Analyses of earlywood pores include only those with an RTA of 116 µm or greater, and solitary or not severely distorted by neighbouring elements. This system of exclusion was adopted because of the extreme range in pore size, from those no larger than parenchyma cells to those with an RTA of over 300 µm. Normally the smaller pores occur in both earlywood and latewood, whereas the larger are found only in earlywood and in the transition between earlywood and latewood. For latewood, only the tangential diameter of pores in the outermost portions of wide growth rings was measured.

Ratios between tangential and radial diameters (T/R) effectively express pore shape and are given in Table 1. A T/R of 1 indicates round, less than one oval, and greater than 1 flattened. Because solitary pores are difficult to confirm in the fossils, this feature has not been emphasised in making comparisons. Means and ranges in pore size do not necessarily reveal the extent of differences between samples. Distribution of size categories, particularly the incidence of larger pores (here defined as those with RTA’s greater than 260 µm) appears to be an important distinguishing feature. Data for large pores (RTA > 260 µm) are recorded in Table 1. It is frequently difficult to distinguish between storied parenchyma and small vessel elements in sectioned material. Because there is little difference in their lengths, the length data for these features are combined and recorded as storied elements (STE) in Table 1. Fibre length was not considered, again because of the difficulty in obtaining measurements from sectioned material, particularly from the fossils.

Preparations of wood from an eastern form of Robinia pseudoacacia (BWCw 8516) and from the western species R. neomexicana Gray (Aw 9542) were included in the study. All fossil specimens will be deposited in the University of California Museum of Paleontology under the catalogue numbers UCMP 12732 through UCMP 12739. Specimens described herein will be identified by the letters DSR (Dove Spring Robinia, 5 samples) or SVR (Stewart Valley Robinia, 4 samples) plus the last two digits of their catalogue number.

**Descriptions**

Data for both extant and fossil specimens are summarised in Table 1 and Figure 17. A detailed description of the California specimens of extant *R. pseudoacacia* (VMP8900) is presented first. Since the fossils possess all the essential features of the wood of *Robinia*, only pertinent quantitative differences and ring characteristics will be discussed in detail. Descriptions of *Robinia pseudoacacia* woods are also given by, e.g., Panshin and De Zeeuw (1980), Grosser (1977), and Selmeier (1979, 1984).

**Extant woods**

VMP8900 – Trunk (Figs. 1, 2, 4) — Three distinct zones are evident in transverse sections of wide growth rings, earlywood (Fig. 1), transition (Fig. 2), and latewood (Fig. 1). The earlywood is characterised by a concentration of mostly large pores in 2 or more loosely defined rows. The pores are solitary or in multiples of various sorts and vary greatly in size (RTA 24–348 µm). The largest pores are not always the first-formed of a season, particularly in wide rings; in fact, small, round, solitary pores are not infrequent among the earliest portions of a growth increment. Parenchyma is abundant, paratracheal to confluent, and, in earlywood, forms most of the ground tissue. In wide rings the loosely arranged pores of earlywood are succeeded in the transition zone by more widely spaced pores which are mostly in multiples. Multiples in the early portions of the transition zone consist mainly of a large pore surrounded by several much smaller ones (Fig. 2). In the latewood all pores are small. Parenchyma in the transition zone is paratracheal (surrounding the clusters rather than individual pores) aliform and occasionally confluent. The relative width of the transition zone varies with the growth ring. In some wide rings it may comprise as much as 50%, whereas it may be absent in narrow rings. Pores in latewood are very small (16–36 µm in tangential diameter) and radially aligned in well-defined clusters. These clusters are surrounded by confluent parenchyma that links neighbouring clusters to form short tangential or diagonal bands within a background of thick-walled fibres. Vessel perforations are simple, inter-
vessel pits alternate and vented. Pits to ray cells are similar in size and distribution. Walls of small vessels have spiral thickenings. Thin-walled tyloses occlude all but the smallest vessels, however even these may contain a single tylose. Parenchyma cells are fusiform or in strands of mostly 2 in earlywood and 2–4 in transition and latewood (Figs. 4, 16). Parenchyma and narrow vessel elements are storied, but wide vessel elements often are not storied.

Multiseriate rays are 2–6 cells wide, cells are procumbent except for occasional uniseriate margins of square cells. Ray height varies widely, but the highest usually occur in earlywood. Those in earlywood are often heterocellular and irregular in outline (Fig. 4), and those in latewood are usually homocellular and spindle-shaped in tangential section. Uniseriates are infrequent in the samples examined. Chambered crystals are abundant in the parenchyma of some areas, particularly in the last formed latewood.

Narrow rings in the outermost portion of the trunk (Fig. 6) were somewhat different from the wider rings described above. Although there is little difference in average size and frequency of earlywood pores, there is a size distribution difference. In narrow rings 61% of the vessels exceed an RTA of 200 μm, but in narrow rings only 42%. A higher proportion of earlywood pores in narrow rings are also radially flattened, and storied elements somewhat longer. The greater average height of rays may be a consequence of the predominance of earlywood in narrow rings. Average ray width differs little, but the number of those 5 or 6 cells wide is 20% greater in wide rings. The differences noted between outermost narrow rings and inner wide rings may be due to declining vigour of the tree, to cambial age, and/or to altered environmental conditions.

Branch (Fig. 3) — The most noticeable differences between stem and branch wood are in shape, size, and distribution of earlywood pores, and in the frequency of solitary pores. Growth rings are narrow in the branch.

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Legends of Figures 1–16:

Figs. 1–4. Robinia pseudoacacia, sample VMP8900. — 1 & 2: Transverse sections of wide growth ring of trunk wood; 1: at earlywood and latewood boundary (arrows indicate latewood pore clusters); 2: transition wood. — 3: Transverse section of branch. — 4: Tangential section through earlywood. — Scale bar (see Fig. 1): Figs. 1–3 = 300 μm; 4 = 120 μm.

Figs. 5 & 6. Robinia pseudoacacia, sample VMP8900. — 5: Transverse section of large root. — 6: Narrow outer rings of trunk. Note absence of tyloses. — Figs. 7 & 8. Miocene Robinia zirkellii, from Dove Spring, California, U.S.A. — 7: Transverse section of widest ring of DSRT. — 8: Transverse section of DSR35 showing diffuse-porous arrangement. — Scale bar (see Fig. 5): Figs. 5, 6, 8 = 300 μm; 7 = 278 μm. Arrows indicate latewood pore clusters.

Figs. 9–12. Miocene Robinia zirkellii, from Dove Spring, California, U.S.A. — 9 & 10: Sample DSR33, transverse sections; 9: wide ring; 10: narrow ring. Arrows indicate latewood pore clusters. — 11: Sample DSR32, latewood vessel element showing what are interpreted as pit vestures. — 12: Sample DSR34, transverse section. — Scale bar (see Fig. 9): Fig. 9 = 290 μm; 10 = 125 μm; 11 = 28 μm; 12 = 260 μm.

Figs. 13–16. Miocene Robinia zirkellii (13–15 from Stewart Valley, Nevada, 16 from Dove Spring, California, U.S.A.). — 13 & 14: Sample SVR36, transverse section of wide rings. Arrows indicate latewood pore clusters. — 15: Sample SVR39, transverse section of narrow ring. — 16: Sample DSR37, tangential view of latewood storied elements and spindle-shaped rays. — Scale bar (see Fig. 13): Fig. 13 = 84 μm; 14 = 290 μm; 15 = 300 μm; 16 = 120 μm.
Extant and fossil Robinia wood anatomy

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samples studied, therefore there is only a small amount of latewood and little or no transition wood. The mostly solitary pores in the earlywood are arranged in a single or occasionally double layer, and are mostly round or oval in reaction wood and round or slightly flattened in abaxial (lower) and lateral portions. The maximum pore size is less than that in trunk wood, particularly in upper and lower areas of the branch. Both average and maximum element length of wide vessels are less in the branch (Table 1).

**Root** (Fig. 5) — Growth rings in the large root are as much as 7 mm wide and discernible to the naked eye. In the small root, rings are narrow and consist chiefly of earlywood. Both large and small roots appear diffuse to semi-ring-porous. Distinctions between rings in areas where they are narrow are lost, because all pores are about the same size and are randomly distributed. Large pores are solitary (up to 60%) or in multiples. All other pores are in small clusters or radially aligned multiples in which most components vary little in size and shape and tend to be less angular than their counterparts in trunk wood. The pattern is most like that in late portions of transition wood but with a higher density of pore clusters. Pores in the large root are mostly round or oval, but in the small root many (35%) are flattened to some degree. Compact clusters typical of the latewood in trunk and branch are not common.

In general, earlywood pores are larger in the root than in the trunk or branch, that is, a higher proportion have an RTA greater than 260 μm (Table 1). Vessel elements in earlywood are somewhat longer, but little difference was noted in the height of multiseriate rays (Fig. 17). Although the average width is not significantly different, there is a higher frequency of narrow rays and uniseriates are more common in the root than in either branch or trunk wood. Parenchyma is abundant, particularly in earlywood where the pattern is similar to that in the rest of the tree. Latewood multiples are accompanied by irregular amounts which occasionally become aliform but rarely confluent, hence diagonal or tangential bands were not observed. Crystals are abundant.

**Summary** — Accepting data from trunk wood as a standard, branch wood deviated from the norm in its smaller pores, higher incidence of round and flattened pores in the earlywood, somewhat shorter earlywood vessel elements, and in the case of the abaxial area, narrower rays. The root differs primarily in the longer earlywood elements and storied elements and the narrower average width of rays. However, data in Table 1 do not reveal all the pertinent differences. The large earlywood pores are mostly solitary and in one layer in branch wood, whereas in trunk wood they are usually in 2 or 3 or more layers, depending on the width of the growth ring, and a higher percentage may occur in multiples. The roots differ from both trunk and branch material in that clusters of small pores are uncommon, the wood is diffuse- or semi-diffuse-porous, and diagonal or tangential bands are not apparent in latewood. Average ray height is greater in the earlywood than in the latewood of all parts of the plant. Two-celled parenchyma strands are more common in earlywood.

The above descriptions clearly show that no one part of the tree illustrates the full extent of anatomical variation in that tree. The assembled data parallel the findings of Gasson (1987) for a ring-porous oak (*Quercus robur*). It is important, therefore, for paleobotanists to be aware of such variability both in initial sampling and in interpretation of resulting data. For example, when comparing data from two transverse sections cut from the same fossil specimen, a 50% difference in the number of oval pores was found. A larger number of round or flattened pores occurred in the same area of each slide where the growth rings narrowed to half the width in the other part. By chance, measurements were taken from the wider portion of the ring in one slide and the narrow portion of the ring in the other. In another instance significant differences in size distribution of pores were documented not only between the large and small roots, but also among different samples of the large root. To illustrate, data for the percentage of pores with an RTA greater than 200 μm and also 260 μm are presented below. WR denotes wide ring and NR narrow rings.
**Sample** | % RTA > 200 µm | % RTA > 200 µm | #/Sample
---|---|---|---
Large root WR | 40 | 13 | 70
NR 1 | 46 | 11 | 59
NR 2 | 68 | 5 | 70
Small root | 88 | 33 | 51

*BWCw 8516* — This specimen differs from trunk wood of VMP8900 only in its larger earlywood pores. The tangential section did not include earlywood, hence data for ray characteristics were limited.

*Aw 9542* — This sample of *Robinia neo-mexicana* has smaller earlywood pores than those in the samples of *R. pseudoacaciacia*, and its rays are narrower. Helices were observed on the walls of not only the smallest vessels but also in some of the larger as well. Those in the latter are frequently coarse. To determine whether this feature is characteristic of the species, it would be desirable to examine macerated material of specimens from a variety of habitats.

**Miocene Fossil Woods**

*Dove Spring, California* — Fossil wood of *Robinia* was first reported from California by Webber (1933). Her description was based on a single poorly preserved specimen of which only three thin sections remain. New material has made it possible to confirm her identification and to supply additional details. The original thin sections represent the type species Webber designated *Robinia alexanderi* and will be referred to here as the Dove Spring *Robinia* Type (DSRT). A brief description is presented for comparison with the new specimens and with wood of extant species of *Robinia*.

The transverse section (Fig. 7) contains 4 growth rings that are 5–10 mm wide. About half the earlywood pores are in multiples. Preservation is such that it is difficult to identify parenchyma in transverse section, but confluent arrangements were not observed and diagonal bands in latewood seem to consist mainly of clusters of small pores. The small radial and tangential sections include only earlywood. Earlywood parenchyma is less abundant than it is in VMP8900. Convincing evidence of crystals was not observed, although circumstantial evidence could be claimed in the presence of parenchyma strands that consist of more than the usual 2 to 4 cells. Intervessel pits contain dark particles that may be the remains of vestures. Despite apparent differences in abundance and distribution of parenchyma, the wood has the general aspect of that of VMP8900, the sample of *Robinia pseudoacaciacia*.

Growth rings in the four new specimens from Dove Spring are narrow. DSR32 and 33 are probably trunk wood, DSR34 is probably branch wood, and DSR35 may represent trunk wood or possibly a root. DSR32 and 33 differ from the type specimen only in possessing narrow growth rings. In the two specimens it is possible to establish patterns of parenchyma distribution and other features poorly preserved in DSRT. Parenchyma forms the ground tissue in earlywood. As in the wide rings of VMP8900 it is vasicentric, aliform, or confluent in the transition zone. A small amount of confluent parenchyma occurs in the latewood where the amount surrounding the clusters of small vessels is inversely proportional to the size of the clusters which are generally larger than the clusters in VMP 8900 (Figs. 9, 10). Particles in vessel pit apertures in well-preserved areas are interpreted as evidence of vestures (Fig. 11). The lower mean length of parenchyma in DSRT as contrasted with both DSR32 and 33 may be due to sampling, since both latewood and earlywood were available in the new specimens.

DSR34 (Fig. 12) differs in several ways from the other Dove Spring samples. Aside from the narrower growth rings (1–2 mm), earlywood pores are smaller, they are distributed more or less in a single row, and a higher percentage are round or slightly flattened. Storied elements are shorter, rays lower. These are the kinds of differences observed between branch and trunk wood in the extant *Robinia pseudoacaciacia* VMP8900 and suggest that DSR34 is branch wood.

DSR35 (Fig. 8) differs from the other Dove Spring samples in that growth rings are poorly defined, and a banded latewood pattern was not observed. Also, earlywood pores are somewhat larger, particularly in tangential diameter, and storied elements although only slightly longer on average, achieve a greater maximum length. Nearly all earlywood pores
at the growth ring margin are solitary, but vessels are in irregular multiples in the rest of the ring. Some of these multiples are characteristic of latewood of the other Dove Spring specimens, but are not as frequent. Multiseriate rays are narrower on average, and uniseriates are more frequent. Parenchyma is more abundant, forming much of the ground tissue in earlywood but largely aliform elsewhere. These kinds of differences between DSR35 and other Dove Spring specimens are similar to those between aerial and root wood in VMP8900. Such differences, however, can also be observed in wide inner and narrow outer rings in the trunk of VMP8900.

On the basis of quantitative characteristics, DSR35 could be either a stem or a root, but if the scarcity of multiples typical of latewood is a constant feature of the root of *Robinia*, their more frequent occurrence in DSR35 would indicate that it is most likely not a root. The absence of such clusters was also noted in illustrations of root sections of *R. pseudoacacia* in Peterson (1973), and Cutler et al. (1987).

**Stewart Valley, Nevada** — The four specimens from Stewart Valley are not well preserved. The cell walls are highly degraded and in many cases, particularly in SVR36, they are somewhat shriveled (Fig. 14). Nevertheless, it is possible to observe most of the essential features, except in SVR36 from which little information was obtained about the length of rays and storied elements. SVR36 was collected from an in situ stump, the other three samples were fragments, they could be from the same stump or from other trees. The four specimens differ very little from one another except in growth ring width, which varies from 2–4 mm in SVR38 to 4–8 mm in SVR36. The primarily oval pores are loosely clustered in 2 or 3 or more ill-defined layers in the earlywood (Figs. 13, 15). Parenchyma in earlywood is abundant and forms most of the ground tissue (Fig. 15). Parenchyma cells are in strands of 2–4 (Fig. 16). Some may be fusiform, but poor preservation and lateral compression of tissues make such distinctions difficult. Chambered strands containing crystals or their 'ghosts' are common. Because fine wall sculpturing was poorly preserved, spiral thickening could be observed in only a few small vessels in one specimen (SVR39). There is some inconclusive evidence that intervessel pits were vestured. Opaque particles in the apertures of most pits are like those observed in poorly preserved tissues in the Dove Spring specimens. Quantitative differences among the specimens derive from variations in growth ring width, extent of cell wall shrinkage, and, possibly, cambial age. Latewood pores in the latest increments of wide rings of SVR36 are about half the size of those in rings of comparable width of VMP8900 and DSRT.

**Conclusions**

Data summarised in Table 1 and in Figure 17 indicate that elements in the Stewart Valley woods are smaller than in either VMP8900 or the Dove Spring woods, for pores are smaller on average, none has an RTA over 260 μm, storied elements and earlywood vessel elements are shorter, and maximum ray height is lower. To a certain extent shrinkage of cell walls may account for some of the differences. Latewood pores of the latest increments in specimens with wide rings are smaller, and there are fewer pores per cluster in the Stewart Valley specimen than in the Dove Spring woods. Also, the earlywood pores are less crowded in the Stewart Valley sample. With the exception of the root and lower portion of the branch of VMP8900, ray width is about the same in both the extant and the Miocene *Robinia*, but the Dove Spring samples appear to have fewer of the broadest rays.

The Dove Spring wood pattern is closely similar to that of specimens of *Robinia pseudoacacia* studied, particularly the eastern U.S. sample (BWCw 8516). Several differences are apparent between the two extant species. In *R. neomexicana* earlywood vessels are smaller (none exceeding an RTA of 260 μm), vessel elements are shorter and rays narrower. Helical thickenings are present in the walls of some of the larger vessels of *R. neomexicana*, whereas they were observed in only the smallest vessels in *R. pseudoacacia*. Helical thickenings were also observed in only the smallest vessels in the fossils, however their absence in larger vessels could be due to preservation.
Table 1. Variations in selected anatomical features in wood of extant *Robina* and *Robinia*-type fossils.

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<td>203–319</td>
<td>241 (29)</td>
<td>188–299</td>
<td>27</td>
<td>0.86</td>
</tr>
<tr>
<td>DSR 33</td>
<td>226 (32)</td>
<td>162–290</td>
<td>290 (45)</td>
<td>203–348</td>
<td>258 (32)</td>
<td>182–319</td>
<td>57</td>
<td>0.79</td>
</tr>
<tr>
<td>DSR 34</td>
<td>191 (26)</td>
<td>128–244</td>
<td>206 (32)</td>
<td>145–261</td>
<td>198 (25)</td>
<td>159–238</td>
<td>0</td>
<td>0.94</td>
</tr>
<tr>
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<td>243 (32)</td>
<td>116–290</td>
<td>290 (39)</td>
<td>220–377</td>
<td>266 (27)</td>
<td>168–310</td>
<td>63</td>
<td>0.84</td>
</tr>
<tr>
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<td>158 (24)</td>
<td>116–215</td>
<td>227 (34)</td>
<td>145–302</td>
<td>193 (21)</td>
<td>130–237</td>
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<td>0.70</td>
</tr>
<tr>
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<td>183 (24)</td>
<td>116–249</td>
<td>218 (36)</td>
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<td>200 (25)</td>
<td>145–246</td>
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</tr>
<tr>
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<td>199 (23)</td>
<td>162–261</td>
<td>241 (25)</td>
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<td>220 (16)</td>
<td>188–252</td>
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<td>116–249</td>
<td>204 (30)</td>
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<td>191 (22)</td>
<td>145–232</td>
<td>0</td>
<td>0.84</td>
</tr>
</tbody>
</table>

EWTD = tangential diameter of earlywood vessels; EWRD = radial diameter of earlywood vessels; RTA = radial diameter + tangential diameter/2; T/R = tangential diameter/radial diameter earlywood vessels; VEL = vessel element length; RW = ray width in cell number; 1s = uniseriate ray height in cells; WR = wide ring; NR = narrow ring; abx = lower; adx = upper; lat = lateral; DSR = Dove Spring *Robinia*; SVR = Stewart Valley *Robina*.  

T/R

AW9542

DSR type

DSR 32

DSR 33

DSR 34

DSR 35

SVR 36

SVR 37

SVR 38

SVR 39

EWTD = tangential diameter of earlywood vessels; EWRD = radial diameter of earlywood vessels; RTA = radial diameter + tangential diameter/2; T/R = tangential diameter/radial diameter earlywood vessels; VEL = vessel element length; RW = ray width in cell number; 1s = uniseriate ray height in cells; WR = wide ring; NR = narrow ring; abx = lower; adx = upper; lat = lateral; DSR = Dove Spring *Robinia*; SVR = Stewart Valley *Robina*.
Fig. 17. Comparisons of selected quantitative features in wood samples of fossil and extant Robinia: a) storied element length (STE), b) ray height, c) pore diameter, mean to maximum radial/tangential average (RTA). Sequence of numbers from left to right = sequence of samples from top to bottom in Table 1: 1–7. R. pseudoacacia, 1–6: VMP8900; 7: BWCw 8516. – 8. R. neomexicana (Aw 9542). – 9–17. Miocene R. zirkellii, 9–13: Dove Spring; 14–17: Stewart Valley. For each sample the thin vertical line = total range, the thick line = ±/– one standard deviation, the short horizontal bar = the mean.

There is considerable overlap among the extant and fossil specimens in quantitative features such as average RTA, element lengths, and ray height and width (Fig. 17). Although ranking may differ with each feature, in general, the samples fall into a series with the Dove Spring woods at one end and R. neomexicana at the other, with BWCw 8516, VMP8900 and Stewart Valley woods in between. Dove Spring woods and the two
samples of extant *R. pseudoacacia* form a group, Stewart Valley overlaps to a certain extent with both the California *R. pseudoacacia* (VMP8900) and *R. neomexicana* thus distinctions between entities are blurred.

The above observations support the conclusion reached by Matten et al. (1977) that quantitative differences in wood anatomy are often useless in distinguishing species in *Robinia*. They also found a continuum of quantitative features not only among their numerous samples of *Robinia* wood from the Pliocene of Oklahoma and several samples of extant *R. pseudoacacia*, but also among these and Miocene and Pliocene species previously described from North America. The lack of distinctive groupings among these fossil wood species led the authors to propose their consolidation as a single taxon. They also presented cogent arguments for assigning the fossils to the extant genus *Robinia*.

Although features characteristic of *Robinia* wood occur in other families, none possess the combination of vented intervessel pits, storied parenchyma and vessel elements, and numerous thin-walled tyloses. The closest approximation is the wood of *Maclura* (Moraceae) which lacks vented pits.

Since the Dove Spring woods possess all the salient features of the wood of *Robinia* and fall within the range of variation among the quantitative characteristics that define it, they are assigned to *Robinia zirkellii* (Platen) Matten, Gastaldo & Lee. The case for assigning the Stewart Valley woods to *R. zirkellii* is less secure. Although the Stewart Valley woods also possess all the features characteristic of *Robinia*, evidence for vented pits is not conclusive. Nevertheless, they are placed provisionally in the same species. Evidence in support of their identification as *Robinia* lies in the presence of leaflets attributed to *Robinia* and the absence of any evidence of *Maclura* among any leaf flora recovered from Stewart Valley localities (Schorn, unpub. ms.). Moreover, several Miocene localities in western U.S. have yielded putative leaflets and fruits of *Robinia*, but none of *Maclura*.

Although the fossil woods with the *Robinia* structural pattern do not differ enough to justify their separation into distinct species, leaflets and pods that occur in many Tertiary localities may eventually provide clues to the extent of variation throughout its range in space and time. Leaflets of *Robinia* occur at the Stewart Valley site (Schorn, unpub. ms.), but none have been reported from the Dove Spring locality, an unlikely source of leaf remains. Leaflets have, however, been recovered from an older Miocene locality not far from Dove Spring in the Tehachapi Mountains. Axelrod (1939) who described these leaflets as *Robinia*, inferred relationship between them and the wood of *Robinia* described by Webber (1933). Such an inference is within reason despite the gap of 3–4 million years between the two localities, if one agrees that “the flora of any particular time has the strongest relationship with the preceding flora of the same region” (Wolfe 1964). Schorn (unpub. ms.) compared leaflets from the Stewart Valley sites and the older Tehachapi sites and found differences between the two suites that led him to suspect that they represent distinct natural species, but the evidence so far is not clear cut. Specific identification of putative leaves, leaflets or pods of *Robinia* present many problems of the sort that occur in the identification of wood.

A detailed survey of woods of extant *Robinia* species may reveal the kinds of adaptations that have occurred in the genus which may, thereby, indicate how to delimit form species among fossil wood assemblages. At the present time no clear-cut distinctions can be discerned in any fossils exhibiting the *Robinia* structural pattern, even between those from the Eocene of the U.S. (Wheeler & Landon 1992), and the Oligocene (Privé-Gill 1990) and Miocene (Selmeier 1979, 1984) of Europe.

According to McMinn and Maino (1956), *Robinia* today consists of about 8 species, however recent workers recognize only 4 or 5 (Lavin 1987; Mabberley 1987). The genus ranges from eastern and southern U.S. into New Mexico, Nevada, Colorado, Arizona and northern Mexico. The western forms are mainly shrubs or small trees adapted to climates characterised by high summer temperatures and low average precipitation. The smaller pores, shorter elements, and helical sculpturing on vessel walls in the
wood of *R. neomexicana* are characteristic of woods adapted to xeric conditions (Carlquist & Hoekman 1985). The Miocene Stewart Spring woods also have smaller pores, but they grew near the shore of a lake, hence the smaller pores could not be attributed to xeric growth conditions. The wide growth rings in many specimens of both the Stewart Valley and the Dove Spring assemblages indicate that these trees enjoyed a long growing season. The high percentage of transition wood in the wide rings, among the Stewart Valley specimens, suggest that conditions were favourable for most of the growing season. In any case, the Miocene woods show no indication of xeromorphic adaptations.

Wide growth rings in both assemblages appear similar to the wide rings in VMP8900, a tree that grew in a Mediterranean type climate and had access to an ample water supply for part of its existence. When rings of comparable width are compared, those in the Dove Spring specimens show a higher proportion of latewood and a lower proportion of transition wood. For example, a ring 10 mm wide in VMP8900 contains 10% early, 70% transition, and 20% latewood; a ring 9 mm wide in SVR36 contains 12% early, 77% transition, and 10% latewood; and one 9 mm wide in DSRT contains 14% early, 45% transition, and 42% latewood. Such a small sample is an inadequate foundation on which to base conclusions; however, there may be some relationship between environmental conditions and the amount of transition wood formed. The essentially xeromorphic structure of latewood in *Robinia* could be interpreted as an adaptation to the hydraulic stress of late summer, and the mesomorphic transition wood an indication of equable conditions of late spring and early summer. The tree VMP 8900 grew in an area where the growing season is long, temperatures mild for several months of the year, and precipitation normally occurs only during the winter months. It produced rings with a high proportion of transition wood when it was irrigated. When irrigation ceased, the resulting hydraulic stress was reflected in narrower rings and little or no transition wood.

Although currently the geographical range of *Robinia* is limited to a relatively small area of North America, during the Tertiary it ranged from eastern Europe to the U.S. Pacific coast. The earliest evidences of *Robinia* are leaflets from the Late Eocene of Colorado (MacGinitie 1953) and wood from the Late Eocene of Nebraska (Wheeler & Landon 1992). Wood has been described from the Oligocene of France (Privé-Gill 1990), the Late Miocene of Washington (Prakash & Barghoorn 1961; Prakash 1968), Montana (Prakash et al. 1962), Germany (Selmeier 1979, 1984), and the Pliocene of Nebraska (Platen 1908) and Oklahoma (Mattet et al. 1977).

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