Monophyly and relationships of the enigmatic family Peridiscaceae

Douglas E. Soltis1, Joshua W. Clayton1, Charles C. Davis2, Matthew A. Gitzendanner1, Martin Cheek3, Vincent Savolainen3, André M. Amorim4 & Pamela S. Soltis5

1 Department of Botany, University of Florida, Gainesville, Florida 32611, U.S.A. d.soltis@botany.ufl.edu (author for correspondence)
2 Harvard University Herbaria, Department of Organismic and Evolutionary Biology, Cambridge, Massachusetts 02138, U.S.A.
3 Royal Botanic Gardens, Kew, Richmond TW9 3DS, U.K.
4 Departamento de Ciências Biológicas, Universidade Estadual de Santa Cruz, Ilhéus, 46.650-000, Bahia, Brazil
5 Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611, U.S.A.

Peridiscaceae, comprising Peridiscus, Soyauxia, and Whittonia, are an enigmatic angiosperm family of uncertain composition and placement. Although some have placed Soyauxia in other families (e.g., Flacourtiaceae, Medusandraceae), rather than in Peridiscaceae, sequence data for five genes (material of Whittonia could not be obtained) provide strong support for a clade of Soyauxia and Peridiscus. This evidence, combined with the strong morphological similarity of Peridiscus and Whittonia, support a monophyletic Peridiscaceae of three genera. Molecular analyses of a three-gene (rbcL, atpB, 18S rDNA) dataset for 569 taxa indicate that Peridiscus + Soyauxia together with Daphniphyllaceae form a clade that is sister to the rest of Saxifragales. Maximum likelihood and Bayesian analyses of Saxifragales using a five-gene (rbcL, atpB, matK, 18S rDNA, 26S rDNA) dataset place Peridiscaceae (posterior probability of 1.00) Peridiscaceae as sister to the remainder of Saxifragales, albeit without high posterior probability (pp = 0.78). Parsimony places a well-supported Peridiscaceae (100% bootstrap) as sister to Paeoniaceae within a paraphyletic Hamamelidaceae, a placement that may be due to long-branch attraction. Following removal of Paeoniaceae from the dataset, parsimony trees place Peridiscaceae as sister to the remainder of Saxifragales. Although the placement of Peridiscaceae is not well supported in any analysis, molecular data suggest that Peridiscaceae do not have as their closest relatives Saxifragaceae, Iteaceae, Pterostemonaceae, Haloragaceae, or Crassulaceae, but instead are more closely related to woody members of Saxifragales (Altingiaceae, Cercidiphyllaceae, Hamamelidaceae, and Daphniphyllaceae); several morphological features similarly suggest a relationship of Peridiscaceae to these woody families. The low support for the placement of Peridiscaceae is not surprising; previous analyses indicate that Saxifragales underwent a rapid, ancient radiation, and resolving relationships among members of the clade, particularly the basal grade of woody taxa, has been extremely difficult.

KEYWORDS: molecular systematics, Peridiscaceae, rapid radiation, Saxifragales

INTRODUCTION

A brief history of Saxifragales. — The composition of Saxifragales as revealed in recent analyses is one of the major surprises of molecular phylogenetic studies of angiosperms (e.g., Chase & al., 1993; Morgan & Soltis, 1993; D. Soltis & al., 1997a, 2000; Qiu & al., 1998; Hoot & al., 1999; P. Soltis & al., 1999; Savolainen & al., 2000a, b; reviewed in D. Soltis & al., 2005). The order (APG II, 2003) now includes Altingiaceae, Cercidiphyllaceae, Crassulaceae, Daphniphyllaceae, Grossulariaceae, Haloragaceae s.l. (expanded to include Tetracarpaeaceae, Penthoraceae, and Aphanopetalum [formerly of Cunoniaceae]), Hamamelidaceae, Iteaceae, Paeoniaceae, Pterostemonaceae (sometimes included in Iteaceae; APG II, 2003), and Saxifragaceae. The circumscription of Saxifragales based on molecular data departs markedly from previous morphology-based classifications, which placed these families in three different subclasses (e.g., Cronquist, 1981; Takhtajan 1997; Morgan & Soltis, 1993; Qiu & al., 1998; reviewed in Soltis & al., 2005): Altingiaceae, Hamamelidaceae, Cercidiphyllaceae, and Daphniphyllaceae were placed in Hamamelidae; Saxifragaceae, Iteaceae, Pterostemonaceae, Grossulariaceae, Crassulaceae, and Haloragaceae s.l. were treated in Rosidae; and Paeoniaceae were placed in Magnoliidae or Dilleniidae (reviewed in Cronquist, 1981). Several members of Saxifragales were considered closely related in some previous classifications: Saxifragaceae, Grossulariaceae, Iteaceae, Pterostemonaceae, Penthoraceae, and Tetracarpaeaceae were considered
part of a much more broadly defined Saxifragaceae s.l. (Engler, 1930; Morgan & Soltis, 1993), and a close relationship of these families to Crassulaceae was also proposed by Cronquist (1981) and Takhtajan (1987, 1997). Though not linked with these families, Hamamelidaceae, Altingiaceae, Cercidiphyllaceae, and Daphniphyllumaceae have also been considered closely related (e.g., the “lower hamamelids” sensu Walker & Doyle, 1975). Haloragaceae and Paoniaeaceae, however, have never been placed with any members of Saxifragales in any classifications prior to APG (1998) and APG II (2003). Haloragaceae had been placed in or near the rosid order Myrtales (Cronquist, 1981), whereas Paoniaeaceae had been considered closely related to Magnoliaceae (Sawada, 1971), Ranunculaceae (Takhtajan, 1997), or Dilleniaceae (Cronquist, 1981). The inclusion of Aphanopetalum in Saxifragales as part of an expanded Haloragaceae was unexpected. Based on anatomical data Dickson & al. (1994) noted similarities between Aphanopetalum and some of the traditionally recognized Saxifragaceae s.l. (e.g., Cronquist, 1981), including members of Saxifragoideae, a group that is now part of Saxifragales.

Although early, broad analyses of rbcL sequences first revealed the Saxifragales clade (Chase & al., 1993; Morgan & Soltis, 1993; Chase & Albert, 1998), they did not provide bootstrap support (BS) greater than 50% for the clade. Investigation of atpB alone, as well as atpB + rbcL, also indicated a monophyletic Saxifragales, but neither of these studies provided BS > 50% (Savolainen & al., 2000a, b). 18S rDNA alone and 18S rDNA + rbcL ultimately revealed a Saxifragales clade with moderate jackknife support (e.g., D. Soltis & al., 1997b; D. Soltis & Soltis, 1997), and the clade received strong support in analyses of a dataset based on plastid rbcL and atpB and nuclear 18S rDNA (Hoot & al., 1999; D. Soltis & al., 2000).

Enigmatic Peridiscaceae. — Based on anatomical characters, some (Sandwith, 1962) considered Peridiscaceae to comprise three genera: Peridiscus (1 species), Soyauxia (9 species, including 3 undescribed species – Cheek, unpubl. data), and Whittonia (1 species). The three genera have a highly disjunct distribution; Peridiscus and Whittonia occur in northern South America, whereas Soyauxia is native to Africa. However, other authors have not considered these three genera to be members of the same family. Whereas Whittonia and Peridiscus have been considered closely related based on numerous shared vegetative, anatomical, and reproductive characters (e.g., Sandwith, 1962; Metcalfe, 1962; Takhtajan, 1997), the relationships of Soyauxia have been problematic. Soyauxia has variously been considered part of Passifloraceae (Oliver in Bentham & Hooker, 1862–1883; reviewed in Brenan, 1953), Flacourtiaeae (e.g., Sandwith, 1962), or Medusandraceae (Brenan, 1953). Cronquist (1981) and Takhtajan (1997) placed Whittonia and Peridiscus together in Peridiscaceae, and Soyauxia in Flacourtiaeae; Peridiscaceae and Flacourtiaeae were considered closely related members of Violales by both authors.

Based on rbcL, atpB, and 18S rDNA sequence data for Peridiscus, Davis & Chase (2004) suggested that Peridiscaceae should also be included in Saxifragales. However, the phylogenetic position of Peridiscus within Saxifragales was unclear. Because only one of three genera of Peridiscaceae was sampled (Peridiscus) by Davis & Chase (2004), both the monophyly of Peridiscaceae as well as the placement of the family within Saxifragales require additional investigation.

In an effort to clarify the composition of Peridiscaceae and relationships of the family within Saxifragales, we conducted a broad molecular phylogenetic analysis of the angiosperms, as well as focused analyses of Saxifragales, adding sequences of four genes for two genera of Peridiscaceae (Peridiscus and Soyauxia; material of Whittonia could not be obtained) to existing multigene datasets.

**MATERIALS AND METHODS**

**DNA amplification and sequencing.** — We isolated DNA following the general method of Doyle & Doyle (1987). A 750-base pair (bp) section of matK for Soyauxia was amplified using trnK-3914F and 1470R (Johnson & Soltis, 1994); the sequencing primers used were 710F, 934F, and 1470R (Johnson & Soltis, 1994, 1995). PCR products were sequenced in both directions using Beckman-Coulter Dye Terminator Cycle Sequencing Quick-Start kits and a Beckman-Coulter automated sequencer following the manufacturer’s protocols (Beckman Coulter, Inc., Fullerton, CA, U.S.A.). A 1300-bp region of matK was sequenced for Peridiscus using the primers matK-400F, matK-842F, and matK-1390R of Cameron & al. (2001), which approximately corresponds to the 3’ region used by Hili & al. (2003). rbcL and atpB were amplified and sequenced following Savolainen & al. (2000a) except that sequencing reactions were run on an Applied Biosystems 3730 DNA Analyzer. The 18S rRNA gene was amplified with primers 20F and 1324R following the general methods of D. Soltis & al. (1997a). Primers 20F, 1324R, and 461R (5’ TTT GCG CGC CTG CCT TCC 3’; Liz Caddick, pers. comm.) were used for sequencing. A portion (~750 bp) of 26S rDNA was amplified for Peridiscus in four separate pieces using primers N-nc26S1 to 950rev, N-nc26S5 to 1839rev, N-nc26S9 to 2782rev, and N-nc26S11 to 3331rev following Kuzoff & al. (1998); these primers were also used for sequencing. A small portion of Soyauxia was amplified...
and sequenced using N-nc26S9 and 2426rev primers. 18S rDNA and 26S rDNA sequencing reactions were run on an Applied Biosystems 3730 DNA Analyzer.

Alignment and phylogenetic analyses. — Sequences were easily aligned visually by adding them to the existing three-gene, 567-taxon matrix (P. Soltis et al., 1999; D. Soltis et al., 2000) and to the five-gene, 40-taxon Saxifragales matrix (Fishbein et al., 2001; Fishbein & Soltis, 2004). Short regions at the beginning and ends of genes for which sequences were incomplete, as well as several short regions of 26S rDNA that were difficult to align (see Kuzoff et al., 1998) were excluded from the analysis.

Maximum parsimony (MP) analyses were conducted using PAUP* 4.0 (Swofford, 2000). MP analyses of the 569-taxon dataset began with 10,000 random taxon addition replicates with no branch swapping, with one tree saved per replicate. These 10,000 starting trees were then used in a second round of heuristic searches with tree-bisection-reconnection (TBR) branch swapping, MulTrees in effect, holding no more than 10,000 most parsimonious trees. Bootstrap analysis was not conducted given the large size of this dataset.

Parsimony analysis of the five-gene Saxifragales dataset used heuristic searches of 1,000 random addition replicates with no more than 10 trees saved per replicate, TBR swapping, and MulTrees in effect. Bootstrap support (BS; Felsenstein, 1985) was estimated from 1,000 bootstrap replicates using 10 random taxon additions per replicate, TBR branch swapping, MulTrees in effect, and saving all trees. Several different analyses of the Saxifragales dataset were conducted. In our primary analysis, we included all five genes. However, when initial results (below) suggested the possibility of long-branch attraction with the addition of 26S rDNA data, Peridiscaceae and Paeoniaceae were alternately excluded from the five-gene dataset. We also conducted a parsimony analysis in which we excluded 26S rDNA.

We also conducted Bayesian and maximum likelihood (ML) analyses using the five-gene dataset for Saxifragales: one analysis was conducted with all five genes, and a second analysis was conducted with 26S rDNA sequences excluded (as above, for parsimony). MODELTEST v3.7 (Posada & Crandall, 1998) was used to select the best evolutionary model for the Bayesian and ML analyses of Saxifragales. Both the hierarchical likelihood ratio tests (hLRTs) and Akaike information criterion (AIC) selected GTR+I+G as the best-fit model. Bayesian analyses were conducted with the MPI-enabled version of MrBayes 3.1.1 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003; Altekar et al., 2004). The chloroplast and nuclear genes were designated as separate partitions, and all model parameters were unlinked, allowing each partition to optimize parameter values separately. Two independent analyses ran for 5 million generations using four Markov chains sampled every 100th generation. The first 100,000 generations were discarded as burn-in; other parameters were left at default values. Posterior probabilities were calculated using the resulting trees from both runs.

ML analyses were implemented in PAUP* using the GTR+I+G model block generated by MODELTEST. The analysis used a heuristic search with 10 random addition replicates, TBR branch swapping, and the MulTrees option in effect.

Trees and datasets have been deposited in TreeBase.

RESULTS

We obtained 750 bp and 1300 bp of matK for Soyauxia talbotii and Peridiscus lucidus, respectively, and 548 bp and 2930 bp of 26S rDNA for Soyauxia and Peridiscus, respectively. Nearly complete sequences of rbcL, atpB, and 18S rDNA were obtained for Soyauxia. Sequences are deposited in GenBank (Appendix).

Our three-gene analysis using the 567-taxon dataset (P. Soltis et al., 1999; D. Soltis et al., 2000) with sequences added for Peridiscus and Soyauxia confirmed the placement of Peridiscaceae within Saxifragales (tree not shown). In this analysis, Peridiscus and Soyauxia formed a clade and appeared as sister to Daphniphyllum. This clade of Peridiscaceae + Daphniphyllaceae appeared as sister to the remainder of Saxifragales.

The parsimony analysis of the Saxifragales dataset based on all five genes resulted in a single shortest tree and revealed a strongly supported Saxifragales clade (99% BS) consisting of two main subclades (Fig. 1). In the shortest tree obtained, a clade of Peridiscus and Soyauxia is well supported (100% BS); Peridiscaceae, in turn, receive support (84% BS) as sister to a well-supported (100% BS) Paeoniaceae. Peridiscaceae plus Paeoniaceae are nested within a paraphyletic Hamamelidaceae, albeit without support greater than 50%. Peridiscaceae, Paeoniaceae, and Hamamelidaceae appear in a weakly supported (55% BS) clade with Altingiaceae and Daphniphyllaceae (Fig. 1). Ceratophyllaceae are sister to this clade, with Altingiaceae plus Daphniphyllaceae sister to the clade of Hamamelidaceae, Peridiscaceae, and Paeoniaceae.

The second main clade is weakly supported (68% BS) and comprises Crassulaceae, Grossulariaceae, Haloragaceae, Iteaceae, Pterostemonaceae, and Saxifragaceae. Within this clade, each family is strongly supported as monophyletic. A well-supported (99% BS) clade of Crassulaceae + Haloragaceae is sister to a well-supported (99% BS) “Saxifragaceae alliance” (Fishbein et al., 2001; D. Soltis et al., 2005) of Grossulariaceae,
Iteaceae, Pterostemonaceae, and Saxifragaceae. Within the Saxifragaceae alliance, Pterostemonaceae + Iteaceae (100% BS) are sister to a clade (99% BS) of Ribes (the sole member of Grossulariaceae) + Saxifragaceae. These results are consistent with those of the five-gene analysis of Fishbein & al. (2001), without the inclusion of Peridiscaceae.

The branches to Paeoniaceae and Peridiscaceae are each very long relative to most other branches in the parsimony tree (Fig. 1). We therefore conducted additional analyses to explore the possibility that long-branch attraction (Felsenstein, 1978) may have affected the parsimony topology. In one analysis, we removed Paeoniaceae from the five-gene dataset; in the shortest tree obtained, Peridiscaceae are sister to the remainder of Saxifragales (tree not shown), albeit without support greater than 50%. In a second analysis, Paeoniaceae remained in the dataset, and we excluded Peridiscaceae. In this analysis, we recovered a single tree that resembled the five-gene tree of Fishbein & al. (2001), with a clade of Cercidiphyllaceae, Altingiaceae, Daphniphyllaceae, Hamamelidaceae, and Paeoniaceae.

Given that only partial 26S rDNA sequences were obtained for Peridiscaceae (particularly Soyauxia), we also explored the impact of the 26S rDNA sequence data. Parsimony analysis of a dataset from which 26S rDNA sequences were excluded resulted in a topology that differed from that described above. Saxifragales are again

![Fig. 1. Shortest tree resulting from parsimony analysis of a five-gene dataset for Saxifragales (length = 6157; consistency index [CI] = 0.521; retention index [RI] = 0.616). Numbers above branches indicate branch lengths; numbers below branches are bootstrap values. Arrows place bootstrap values on short branches.](image-url)
well supported (BS 100%) as a clade, but a well-supported Peridiscaceae (BS 100%) appear as sister to the remainder of Saxifragales, albeit without BS greater than 50% (tree not shown). Daphniphyllaceae now appear as part of a pentachotomy that also includes: (1) Hamamelidaceae, (2) Cercidiphyllaceae, (3) Altingiaceae, and (4) a large clade of Grossulariaceae, Saxifragaceae, Iteaceae, Pterostemonaceae, Paeoniaceae, Crassulaceae, and Haloragaceae.

In the Bayesian analysis of the five-gene dataset (Fig. 2), Peridiscaceae, represented by *Peridiscus* and *Soyauxia*, are again sister taxa (posterior probability [pp] = 1.0). Peridiscaceae are sister to the remainder of Saxifragales. The remaining members of the order form two clades. One of these clades (pp = 0.82) consists of a trichotomy of Cercidiphyllaceae + Daphniphyllaceae (pp = 0.75), Altingiaceae (pp = 1.0), and Hamamelidaceae (pp = 1.0). The second clade (pp = 0.88) consists of Paeoniaceae as sister to a clade of the remaining Saxifragales (pp = 0.92), which comprise a clade (pp = 1.0) of Crassulaceae + Haloragaceae as sister to a clade (pp = 1.0) of (Iteaceae + Pterostemonaceae; pp = 1.0) + (Grossulariaceae + Saxifragaceae; pp = 1.0) (Fig. 2).

Maximum likelihood resulted in a topology (tree not shown; –lnL = 46,746.02229) identical to the Bayesian tree.

When 26S rDNA sequence data were removed, Bayesian and ML analyses placed a clade (pp = 0.68) of

---

**Fig. 2.** Majority rule consensus showing the posterior probabilities (above branches) based on Bayesian analysis of a five-gene dataset for Saxifragales (see Methods for details). Arrows place pp values on short branches.
Peridiscaceae (pp = 1.0) + Daphniphyllaceae as sister to the remainder of the order. Peridiscaceae + Daphniphyllaceae were subsequently followed by a grade of Hamamelidaceae, Altingiaceae, and Cercidiphyllaceae as sister to a clade of Paeoniaceae plus the remaining Saxifragales (Crassulaceae, Haloragaceae, Itaceae, Pterostemonaceae, Grossulariaceae, and Saxifragaceae). Relationships among members of the Hamamelidaceae, Altingiaceae, and Cercidiphyllaceae grade have pp values below 0.80. In contrast, relationships among Crassulaceae, Haloragaceae, Itaceae, Pterostemonaceae, Grossulariaceae, and Saxifragaceae were again well supported (pp = 1.0) and identical to those described above.

**DISCUSSION**

Our phylogenetic analyses support the hypothesis (Sandwith, 1962) that Peridiscaceae comprise *Whittonia*, *Peridiscus*, and *Souyaxia*. Whereas *Whittonia* and *Peridiscus* are morphologically similar and have been considered closely related (e.g., Metcalfe, 1962), the relationships of *Souyaxia* have been problematic. For example, Cronquist (1981) and Takhtajan (1997) both placed *Whittonia* and *Peridiscus* together in Peridiscaceae, but *Souyaxia* was placed in Flacourtiaceae. Molecular data firmly place *Souyaxia* with *Peridiscus* and, combined with the strong morphological similarity of *Peridiscus* and *Whittonia*, support a monophyletic Peridiscaceae of three genera. Several distinctive morphological features are also shared by all three genera of Peridiscaceae. For example, the endosperm walls are massively thickened in genera of Peridiscaceae (Sandwith, 1962; Stevens, 2004). Genera of the family also have a distinctive petiolar anatomy (Metcalfe, 1962; Stevens, 2004).

Broad analysis of a three-gene, 569-taxon dataset for angiosperms (D. Soltis & al., 2000) confirms the placement of Peridiscaceae within Saxifragales (Davis & Chase, 2004); Peridiscaceae appear as sister to Daphniphyllaceae; this clade is, in turn, sister to the remainder of Saxifragales.

Five-gene analyses of Saxifragales suggest that Peridiscaceae may be sister to the remainder of Saxifragales. Bayesian and ML searches of the five-gene dataset place Peridiscaceae as sister to the remainder of the clade (Fig. 2). Parsimony analyses appear to be affected by long-branch attraction (Fig. 1), with Peridiscaceae and Paeoniaceae (both on very long branches) forming a clade nested within Hamamelidaceae. Long-branch attraction may have similarly affected the parsimony analysis of Saxifragales by Davis & Chase (2004). Their analysis, based on *rbcL*, *atpB*, and 18S rDNA, also placed Peridiscaceae (represented in that study only by *Peridiscus*) as sister to Paeoniaceae. Significantly, when we removed Paeoniaceae from our five-gene dataset, parsimony places Peridiscaceae as sister to the remainder of Saxifragales. When Peridiscaceae are removed, Paeoniaceae are sister to Daphniphyllaceae (and part of a clade that includes Altingiaceae, Hamamelidaceae, and Cercidiphyllaceae). This is the same topology recovered in the five-gene analysis of Fishbein & al. (2001); these results further support our hypothesis that the parsimony placement of Peridiscaceae and Paeoniaceae in our five-gene analysis is the result of long-branch attraction. Removal of 26S rDNA sequence data provides additional support for a basal placement of Peridiscaceae; when these data are removed, the parsimony tree is like the Bayesian and ML trees with Peridiscaceae sister to the rest of Saxifragales.

However, none of the interfamilial relationships noted receives BS greater than 50% or a high posterior probability. Although our analyses clearly indicate that a monophyletic Peridiscaceae are part of Saxifragales, and typically place Peridiscaceae as sister (either alone or with Daphniphyllaceae) to the rest of Saxifragales, molecular data have so far not identified a well-supported placement of the family. Perhaps one noteworthy result is that Peridiscaceae are not part of the large clade of Crassulaceae, Haloragaceae, Itaceae, Pterostemonaceae, Grossulariaceae, Saxifragaceae. Instead our data suggest that Peridiscaceae may be part of a clade or grade of woody taxa that includes Cercidiphyllaceae, Daphniphyllaceae, Hamamelidaceae, and Altingiaceae. Relationships among the woody families of Saxifragales, including Peridiscaceae, remain largely unresolved, a result that may be attributable to an early, rapid radiation in the clade (Fishbein & al., 2001). As also noted by Fishbein & al. (2001), it may require a large number of additional base pairs to resolve deep-level phylogenetic relationships in Saxifragales.

Are there morphological characters that unite members of Peridiscaceae with other Saxifragales? As reviewed elsewhere (e.g., D. Soltis & al., 2005), the morphological diversity encompassed by Saxifragales is large, as seen in the comparison of features in Table 1. As a result, it is hard to identify features that are synapomorphies for the clade. However, the woody members do share a suite of anatomical characters (Table 1). Daphniphyllaceae, Hamamelidaceae, Altingiaceae, and Cercidiphyllaceae all possess vessels with scalariform perforation plates, imperfect tracheary elements with distinctly bordered pits, and wood parenchyma that is apotracheal and diffuse (Baas & al., 2000) (Table 1). Peridiscaceae, although poorly studied, also exhibit these same anatomical features (Table 1) (Metcalfe, 1962; see Cronquist, 1981; Stevens, 2004). In contrast, these features either do not occur, or occur rarely in other Saxifragales (represented by Crassulaceae in Table 1), which are primarily herbaceous (e.g., Crassulaceae,
Saxifragaceae), or shrubs (e.g., Iteaceae, Grossulariaceae). For example, whereas Daphniphyllaceae, Hamamelidaceae, Altingiaceae, and Cercidiphyllaceae have vessels with scalariform perforation plates, other families of Saxifragales typically have simple perforation plates (Aphanopetalum) also has scalariform perforation plates; both simple and scalariform perforation plates have been reported in Paioniaceae).

Other morphological features are also shared by woody Saxifragales. Peridiscaceae, Altingiaceae, Cercidiphyllaceae, Daphniphyllaceae, and Hamamelidaceae all possess pendulous ovules (Table 1), a feature found infrequently elsewhere in Saxifragales (e.g., Haloragaceae). Peridiscaceae also exhibit a tanniniferous layer of cells in the tegmen, a feature also found in other woody Saxifragales, including Cercidiphyllaceae, Daphniphyllaceae, and Hamamelidaceae (Table 1).

A possible feature uniting Peridiscaceae with other Saxifragales may be ovary position and gynoecial development. Typically, ovary positions have been described as superior versus inferior, and decisions concerning structural homology made exclusively on the basis of anthetic (i.e., mature) floral structure. Ovary position varies in Peridiscaceae. The gynoecium of Peridiscus is half-inferior, described as half-sunken into the disk (Sandwith, 1962), whereas flowers of Whittonia and Soyauxia are described as hypogynous (Brenan, 1953). This degree of variation in ovary position among related genera is also seen in other Saxifragales. For example, in Saxifragaceae, the complete range of ovary positions

Table 1: Morphological comparison of Peridiscaceae with some representative families of Saxifragales (modified from Davis & Chase, 2004; characters taken from Cronquist, 1981; Baas & al., 2000; D. Soltis & al., 2005; Stevens, 2004).

<table>
<thead>
<tr>
<th>Character</th>
<th>Peridiscaceae</th>
<th>Daphniphyllaceae</th>
<th>Hamamelidaceae</th>
<th>Altingiaceae</th>
<th>Cercidiphyllaceae</th>
<th>Crassulaceae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primary veins</td>
<td>palmate</td>
<td>pinnate</td>
<td>palmate</td>
<td>palmate</td>
<td>palmate</td>
<td>palmate</td>
</tr>
<tr>
<td>Stomates</td>
<td>anomocytic</td>
<td>paracytic</td>
<td>various</td>
<td>paracytic</td>
<td>imperforate with</td>
<td>imperforate</td>
</tr>
<tr>
<td>Stipules</td>
<td>present</td>
<td>absent</td>
<td>present</td>
<td>present</td>
<td>bordered pits</td>
<td>with simple</td>
</tr>
<tr>
<td>Scalariform perforation plates</td>
<td>present</td>
<td>absent</td>
<td>mostly present</td>
<td>present</td>
<td>apotracheal,</td>
<td>pits</td>
</tr>
<tr>
<td>Tracheary elements</td>
<td>imperforate with bordered pits apotracheal, diffuse axillary racemes</td>
<td>imperforate with bordered pits apotracheal, diffuse spikes (seldom racemose or paniculate)</td>
<td>imperforate with bordered pits apotracheal, diffuse racemes; globose head</td>
<td>imperforate with bordered pits apotracheal, diffuse terminal on sympodial short shoots</td>
<td>imperforate with simple pits</td>
<td></td>
</tr>
<tr>
<td>Wood parenchyma type</td>
<td>palisade</td>
<td>diffuse</td>
<td>mixed</td>
<td>diffuse</td>
<td>absent</td>
<td>absent</td>
</tr>
<tr>
<td>Inflorescence type</td>
<td>2–6, imbricate</td>
<td>4–5(–10), imbricate</td>
<td>4–5(–10), anther dehiscence by slits</td>
<td>4–10, dehiscence by slits</td>
<td>4–5(–10), anther dehiscence by slits</td>
<td>usually 5</td>
</tr>
<tr>
<td>Petals</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
<td>absent</td>
</tr>
<tr>
<td>Floral subtending bract</td>
<td>4–7, imbricate</td>
<td>2–6 (rarely absent), imbricate</td>
<td>2–9(–5), imbricate</td>
<td>4–10, dehiscence by slits</td>
<td>4–10, dehiscence by slits</td>
<td>usually 10, dehiscence by slits</td>
</tr>
<tr>
<td>Sepals</td>
<td>4–7, imbricate</td>
<td>2–6 (rarely absent), imbricate</td>
<td>2–9(–5), imbricate</td>
<td>4–10, dehiscence by slits</td>
<td>4–10, dehiscence by slits</td>
<td>usually 10, dehiscence by slits</td>
</tr>
<tr>
<td>Stamens</td>
<td>3–4</td>
<td>2(–4)</td>
<td>2(3)</td>
<td>2</td>
<td>1</td>
<td>3–10</td>
</tr>
<tr>
<td>Carpel number</td>
<td>half inferior</td>
<td>superior</td>
<td>half to fully inferior</td>
<td>half inferior</td>
<td>does not apply in at there is no perianth</td>
<td>superior</td>
</tr>
<tr>
<td>Ovary position</td>
<td>short</td>
<td>short</td>
<td>long</td>
<td>short</td>
<td>long</td>
<td>long</td>
</tr>
<tr>
<td>Style length</td>
<td>pendulous from top of the ovary one seeded drupe</td>
<td>pendulous from top of the ovary one seeded drupe</td>
<td>pendulous from top of the ovary capsule</td>
<td>pendulous from top of the ovary capsule</td>
<td>in two rows</td>
<td>follicle</td>
</tr>
<tr>
<td>Ovules/placentation Fruit</td>
<td>present</td>
<td>present</td>
<td>present</td>
<td>absent</td>
<td>present</td>
<td>absent</td>
</tr>
<tr>
<td>Tanniniferous layer of cells in</td>
<td>present</td>
<td>present</td>
<td>present</td>
<td>absent</td>
<td>present</td>
<td>absent</td>
</tr>
<tr>
<td>the seed tegmen</td>
<td>abundant, walls massively thickened</td>
<td>abundant, oily and proteinaceous</td>
<td>scanty, oily and proteinaceous</td>
<td>scanty</td>
<td>scanty, oily</td>
<td>copious to scanty, oily and proteinaceous</td>
</tr>
<tr>
<td>Endosperm</td>
<td>small</td>
<td>small, straight</td>
<td>large, straight</td>
<td>long</td>
<td>large, spatulate</td>
<td>long</td>
</tr>
</tbody>
</table>
from what has been described as superior to completely inferior, as well as a range of intermediates, has been described within Lithophragma and Saxifraga (Kuzoff & al., 2001; D. Soltis & Hufford, 2002). Studies of floral development in Saxifragaceae and other Saxifragales indicated that species reported to have superior ovaries actually have an appendicul epigynous ground plan, a developmental program that leads to the formation of inferior ovaries (e.g., Kuzoff & al., 2001; D. Soltis & Hufford, 2002). Thus, these ovaries are not truly superior but represent “superior mimics” or “pseudosuperior” ovaries. Appendicul epigyny typifies nearly all Saxifragales and is also plesiomorphic for the clade. Ovaries termed “superior” in Iteaceae and Paeoniaceae are, in fact, pseudosuperior (reviewed in D. Soltis & al., 2005; for floral development in Paeoniaceae see also Hiepko, 1965), derived via an appendicul epigynous ground plan and are comparable to those observed in Saxifragaceae (D. Soltis & al., 2005). In Saxifragaceae and other Saxifragales, ovary position at anthesis is a consequence of the amount of vertical extension of the inferior vs. superior region of the ovary (Kuzoff & al., 2001; D. Soltis & al., 2003). This same flexibility or lability in ovary position development, shown to be responsible for generating variation in ovary position in Saxifragaceae, Iteaceae, and other Saxifragales may also be operating in Peridiscaceae.

In conclusion, our data suggest a monophyletic Peridiscaceae that includes the problematic Soyauxia; molecular data suggest a placement of the enigmatic Peridiscaceae as sister to the remainder of Saxifragales. Resolving the precise placement of the family with any measure of internal support will be a challenge, however, given that all available data suggest that Saxifragales represent an ancient, rapid radiation (Fishbein & al., 2001).

ACKNOWLEDGMENTS

This research was supported in part by an Assembling the Tree of Life (AToL) grant EF-0431266 (NSF). We thank Martyn Powell for his help with DNA sequencing. We thank two anonymous reviewers for their helpful comments.

LITERATURE CITED


Appendix. Species of Peridiscaceae analyzed, collection and voucher data.

Species; collection; location of voucher; GenBank accession number.

Peridiscus lucidus Benth.; Soares 205 (CEPEC); matK: DQ411570; 26S rDNA: DQ400571. Soyauxia talbotii Oliv.; Cheek 10617 (K); matK, 26S rDNA: DQ400572, DQ241372; 18S rDNA: AM111355; rbcl: AM111356; atpB: AM111257.