PALEOSECURIDACA CURTISII GEN. ET SP. NOV., SECURIDACA-LIKE SAMARAS (POLYGALACEAE) FROM THE LATE PALEOCENE OF NORTH DAKOTA AND THEIR SIGNIFICANCE TO THE DIVERGENCE OF FAMILIES WITHIN THE FABALES

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Paleosecuridaca curtisii Pigg, DeVore, and Wojciechowski gen. et sp. nov. (Polygalaceae) is described for anatomically preserved, nonschizocarpic, asymmetric samaras from the Late Paleocene (Tiffanian 3) Almont and Beicegel Creek floras of North Dakota. Paleosecuridaca is quite similar to the extant genus Securidaca L. (Polygalaceae) but has several distinctive features that warrant the establishment of a new genus. Fruits are 2.5–3.6 cm long (x = 3.0 cm, n = 16) with a central ovoid nut 0.6–1.25 cm long (x = 0.9 cm, n = 26), 0.35–0.8 cm wide (x = 0.6 cm, n = 26), and 0.25–0.3 cm thick attached to a broad wing with a small secondary wing on its upper surface. The wing is vascularized by several veins running parallel to its long axis at the top and others in the main body of the wing arching downward and outward, with a few interreticulations occurring between the major veins. The nut contains a single, large locale with two well-developed seeds, each with a seed coat that has a prominent palisade layer like that of many extant genera of Polygalaceae. Specimens lack the broad attachment surface characteristic of Acer and instead have a short peduncle. Paleosecuridaca resembles the compressed fruit Deviacer Manchester from the Paleogene of western North America, Europe, and Asia and may be its anatomically preserved equivalent. The Late Paleocene Paleosecuridaca is the oldest-known megafossil representative of the Polygalaceae, a family now nested within the Fabales (sensu APG II) along with Leguminosae, Surianaceae, and Quillaja Molina on the basis of new molecular data. Together with the earliest record of Leguminosae from the Late Paleocene of Wyoming, these samaras provide independent evidence for an earlier divergence of these two families.

Keywords: Deviacer, Fabales, fossil fruit, Paleocene, Polygalaceae, samara, Securidaca.

Introduction

Asymmetrically winged samaras are a relatively common element of the Tertiary fossil record of the Northern and Southern hemispheres. Like their extant counterparts, fossil samaras represent a wide variety of families, including Sapindaceae sensu lato (e.g., Acer L., Thunia Poit., and Thuninidiul Radl.), as well as Anacardiaceae, Bignoniaceae, Celastraceae, Combretaceae, Leguminosae, Magnoliaceae, Malpighiaceae, Phytolaccaceae, Polygalaceae, Rhamnaceae, Trigoniacaeae, Ulmaceae, and Vitaceae (Burnham 1995; Mirle and Burnham 1999; Burnham and Carranco 2004). Samaras are both structurally and functionally quite variable, and their functional morphology, particularly the biomechanics of dispersal, has been of interest to ecologists for some time (Green 1980; Augspurger 1986; Matlack 1987). Variations in detail of samara attachment and orientation, wing and nut shape, venation, and ornamentation have proved to be taxonomically significant (Mirle and Burnham 1999).

Among the most common types of asymmetric samaras found in the western North American Tertiary are those of the maples (Acer), a group that appears to have radiated during the Eocene. In their monographic study of Tertiary maples, Wolfe and Tanai (1987) recognized a distinctive type of samara that they informally called “Acer arcticum,” which differed from typical Acer in appearing to have dorsally, rather than ventrally, directed wings. They suggested that A. arcticum might represent an extinct type of maple fruit that occupied a transitional evolutionary position, along with fossil Bohlenia Wolfe and Wehr (Wolfe and Wehr 1987), in the radiation that resulted in the two extant genera within this group, Acer and Dipteronia Oliver (Wolfe and Tanai 1987). On the basis of overlapping morphological variation, Bohlenia is now included by some in Dipteronia (McClain and Manchester 2001).

Compressed fruits of the “A. arcticum” type were formally described as Deviacer Manchester from the middle Eocene Clarno Formation (Manchester 1994) and assigned to Sapindaceae sensu lato (Judd et al. 1994). Deviacer also occurs in Eocene localities of the Okanagan Highlands at Republic, Washington (Wehr 1995), and Quilchena, British Columbia, Canada (Mathews and Brooke 1971), as well as in the late Eocene Florissant flora of Colorado (MacGinitie 1953; Manchester 2001) and the Badgers Nose flora of northern California (Myers 2007). Paleocene occurrences are reported from Colorado and Wyoming (Brown 1962), as well as the Lower Eocene of Denmark (Pigg 1980).
et al. 2006), and are also known in Asia (S. R. Manchester, personal communication, 2005).

In this study, we describe Palaeosecuridaca curtisi gen. et sp. nov., an anatomically preserved, nonschizocarpic, asymmetric samara from the Late Paleocene (Tiffanian 3) Almont and Beecegul Creek floras of North Dakota. These fossils, which greatly resemble Deviacer and may be the anatomically preserved equivalent, were previously figured and described briefly from the Almont flora by Crane et al. (1990), who compared them with samaras from Florissant (MacGinitie 1953) and the extinct genera Thouinia and Thouinidium (Sapindaceae), as well as Securidaca (Polygalaceae). Our investigation based on a larger sample of 38 specimens, including several with internal anatomical structure, reveals new details that support the close affinities of these Paleocene samaras with Securidaca (Pigg et al. 2004). This study provides the earliest megafossil evidence for the Polygalaceae, now considered one of three possible families that form the sister group to the legumes (Lavin et al. 2005; Forest et al. 2007). Together with the earliest record of Leguminosae from the Late Paleocene of Wyoming, these samaras provide independent evidence for an earlier divergence of these two families within Fabales sensu APG (2003).

Material and Methods

Samaras are anatomically preserved in silicified shale from two areas in central and western North Dakota (Bluemle 1983, 2000). Most of the specimens studied were collected from the original Almont site in Morton County, central North Dakota (SE1/4 SW1/4 sec. 23 T140N R8W; Crane et al. 1990), and one was obtained from a newly recognized locality near Beecegul Creek, MacKenzie County, ~120 km to the west (Pigg and DeVore 2005). Both collecting sites occur within the Sentinel Butte Formation and are considered Late Paleocene (Tiffanian 3) on the basis of mammal and mollusk correlations (Kihm and Hartman 1991). At both sites, fossils occur in a brownish-tan silicified shale that preserves both external morphological features of leaves and other plant organs and internal anatomy of fruit and seed remains.

Fruits in this study were photographed from fractured surfaces, and selected specimens were embedded in Bio-plastic (Buehler Isomet 1000 saw (Lake Bluff, IL) into sections 0.4–1.0 mm in thickness. Sections were mounted on microscope slides with UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.E., Lakewood, CO), ground if necessary, and covered with a coverslip mounted in UV-cured adhesive (UV-154, T.H.
flora, generosity in sharing specimens, and support of the paleobotanical community.

Description. The description of *Paleosecuridaca curtisii* is based on 38 specimens, 37 from the original Almont locality in Morton County, North Dakota, and one from Beicegel Creek, MacKenzie County, North Dakota. The nonschizocarpic samaras (fig. 2A, 2C–2H; fig. 3A, 3C–3G) are markedly similar to extant *Securidaca* (fig. 2B; fig. 3B, 3H, 3I; fig. 4A). As is typical with Almont specimens, fossils have excellent morphology, with only occasional anatomical structure of some fruits. Of the many specimens that were fractured through the fruit wall and seed coat (e.g., figs. 2C, 3A), several contain details of fruit and seed anatomy (fig. 3A, 3C–3G). Others that appeared complete on initial study were discovered to be mud casts after they were sectioned. Intact specimens are well enough preserved to compare in detail with extant fruits.

Fruits are asymmetrical samaras that range from 2.5 to 3.6 cm long ($x = 3.0 \text{ cm}, n = 16$; fig. 2A, 2C–2H). They contain an ovoid nut 0.6–1.25 cm long ($x = 0.9 \text{ cm}, n = 26$), 0.35–0.8 cm wide ($x = 0.6 \text{ cm}, n = 26$), and 0.25–0.3 cm thick (fig. 2A, 2D, 2E, 2H). The nut is typically positioned at a downward angle in relation to the wing (fig. 2A, 2D, 2E, 2G), although in some specimens, the angle may be almost parallel to the wing (fig. 2F, 2H).

The nut is attached to a broad wing that ranges from 1.7 to 2.5 cm long ($x = 2 \text{ cm}, n = 16$) and 0.6–1.15 cm high ($x = 0.96 \text{ cm}, n = 20$). Wings have a straight top margin and vary in the shape of the lower margin (fig. 2A, 2C–2E, 2H). The veination of the wing consists of several veins on the upper side running parallel to its long axis and venation within the body of the wing arching downward and outward with relatively few interreticulations (fig. 2A, 2D). A small secondary wing is formed apically on the nut and is positioned parallel to the long axis of the nut (fig. 2F, 2G).

Specimens lack the broad attachment surface of *Acer* and other schizocarpic samaras, and instead, many are attached to an elongate peduncle up to 7 mm long at the proximal surface, which represents the point of attachment to the parent plant (fig. 2A, 2E, 2F, 2H). The peduncle contains small vascular elements with helical patterns (fig. 3F) and larger ones with scalariform patterns (fig. 3G). There is no evidence of perianth or style. Several blocks containing specimens of *Paleosecuridaca* also show remnants of stem fragments in the matrix; however, we have yet to find any of these attached to the fruit peduncles.

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Fig. 1 A, Line diagram showing two seeds (numbered) within a single locule in *Paleosecuridaca*. Parallel lines represent prominent palisade layer of seed coat; dashed lines to inside are the inner seed coat layer. Checkered area at left is fruit wall; solid line to inside is the inner boundary of the fruit wall. Circular structures are positions of drusy quartz crystals formed during diagenesis. Drawn from PP 34562 (fig. 3A), ×15. B–D, Line diagrams showing the organization of *Paleosecuridaca*, Polygala, and Securidaca* fruits in transverse section. B, *Paleosecuridaca* fruit with one locule containing two seeds. C, Polygala fruit with two locules, each with a single seed. D, *Securidaca* fruit, with one locule containing a single seed and an area at left designating the abortive locule. C, D, Redrawn from Krüger et al. (1988).
In transverse section, the samara shows a fruit wall surrounding a single locule bearing two seeds (fig. 1A, 1B; fig. 3A). The fruit wall is poorly preserved, but in some areas, it is sufficient to demonstrate an outer zone of spongy parenchymatous tissue and, to the inside, a zone of smaller, thick-walled cells (fig. 3C, 3D). Each of the seeds has a prominent outer seed coat of very thin, radially elongate palisade cells (fig. 3E). They are highly crushed but can be reconstructed on the basis of the

Fig. 2  Samaras of Paleosecuridaca curtisii Pigg, DeVore, and Wojciechowski gen. et sp. nov. and extant Securidaca fruits for comparison. A, C–H, Paleosecuridaca curtisii. B, Extant Securidaca. A, Specimen showing general features of Paleosecuridaca, UWSP 3149, ×2. B, Extant Securidaca longipedunculata Fres. samara showing general features, specimen Sensei 3309 (K), ×1.8. C, Holotype specimen, PP34562, ×2.8. D, Complete samara with smaller peduncle and secondary wing. Previously figured as fig. 23C in Crane et al. (1990), PP34197, ×2.2. E, Specimen showing prominent peduncle, which appears to be wrapped around another “string,” UWSP 3329, ×2. F, Samara showing prominent peduncle, UWSP 2674, ×2.3. G, Samara showing detail of venation across surface of smaller nut wing on upper nut surface, UWSP 3677, ×10. H, Samara with prominent peduncle, ASU 1600, ×3.7.
Fig. 3  Fruit and seed anatomy of Paleosecuridaca and extant Securidaca longepedunculata. A, C–G, Paleosecuridaca. B, H, I, Extant S. longipedunculata. A, Oblique transverse section through holotype specimen showing remains of two seeds within a single locule (numbered). See fig. 1A for details, PP34562, ×12. B, Extant S. longepedunculata samara sectioned longitudinally to show single seed in large locule and smaller, abortive locule (upper left), specimen Trocein 1182 (K), ×4.4. C, SEM of fossil fruit wall showing its spongy nature, UWSP 3149, ×88. D, Detail of fruit wall from specimen in figs. 2C, 3A, and 3E showing spongy nature. Compare with C, P34562, ×90. E, Detail of holotype specimen (A) showing prominent palisade layer of the seed coat (center), opalized cast of the embryo cavity (at right), and fragments of fruit wall (at left),
orientation of distinctive very thin palisade cells 150 μm high and 25 μm wide and an inner seed coat with three to five rows of tangentially elongate cells (fig. 1A; fig. 3A, 3E). Embryo cavities are filled with opalized casts and occasional drusy quartz formed during diagenesis. There is no evidence of the embryo.

Discussion

Establishment of the New Taxon

Paleosecuridaca curtisii Pigg, DeVore, and Wojciechowski gen. et sp. nov. is established for anatomically preserved, asymmetric, nonchizocarpic samaras that greatly resemble the extant genus Securidaca (Polygalaceae). The morphological features bear a superficial resemblance to several extant samara types, including Securidaca, Thoubinia, and Thoubinidadium. A closer analysis shows greater similarities to Securidaca on the basis of (1) a lack of a broad attachment surface that would be expected in schizocarpic samaras; (2) the presence of a peduncle; (3) the presence of a wing with parallel venation apically that curves downward and outward in the body of the wing, with occasional interreticulations; (4) a proximal locule position with respect to the wing; and (5) presence of a small wing on the upper surface of the nut. Unlike fruit morphologies observed among Sapindaceae, these Almont samaras lack the fusion of two to three samaras along the broad upper surface, and there is no evidence of a distal style.

Securidaca is the only genus within the Polygalaceae with species that consistently have a well-developed samara. Some species of Momnina Ruiz and Pavon subgenus Pterocarya may also have samaras; however, fruits in this genus range from being distinctively winged to wingless, a condition that Eriksen (1993b) suggests is either pleisomorphic or derived within the genus. In species of Momnina where the wing is fully developed, it is symmetrical rather than asymmetrical, as in Securidaca.

Anatomical details also show affinities of Paleosecuridaca to Polygalaceae with fruit and seed anatomy, including a spongy mesocarp and a prominent palisade layer of the outer seed coat (Verkerke and Bouman 1980). However, in the character of a prominent palisade layer, Paleosecuridaca differs from extant Securidaca, which lacks a well-developed palisade and is more like several other genera in Polygalaceae, such as Polygala L. and Nylandtia Dumort. (Corner 1976; Verkerke 1985). The prominent palisade layer is derived from varying combinations of developmental layers in different genera of Polygalaceae and varies in origin even among different sections of the large genus Polygala (Verkerke and Bouman 1980), suggesting that this feature may have originated more than once in the family.

The additional characters of number of locules and number of seeds per locule are also significant in Paleosecuridaca.

Unlike all extant Polygalaceae, Paleosecuridaca has two seeds of equal size within a single locule (fig. 1A, 1B; fig. 3A). The mature fruit of Securidaca and most of the species of Momnina are pseudomonomorous as a result of the development of only one of the two carpels (Leinfellner 1972; Krüger and Robbertse 1988; Krüger et al. 1988; Eriksen 1993a). Other fruits in Polygalaceae typically have two locules, each with a single ovule (Verkerke 1985), although Carpolobia G. Don. may have three uniovulate locules and several other genera, including Nylandtia, have a single uniovulate locule (Persson 2001; Forest et al. 2007). Members of tribe Xanthophyllaeae Chodat, which apparently forms the sister group to the rest of the family (Forest et al. 2007), can have four to 40 ovules per carpel. All genera of Surianaceae, a family closely related to Polygalaceae within Fabales, have the biovulure condition. Thus, although Paleosecuridaca has unilocule, biovulate fruits that are unknown among extant Polygalaceae, this condition is characteristic of a sister family. Together these differences from extant Securidaca, (1) the presence of a prominent palisade layer in the seed coat and (2) the uniloculate, biovulate condition, result in a fruit that we consider distinctive enough to recognize as a new genus that we name Paleosecuridaca in light of its closest resemblance to this modern taxon.

Because perianth parts or scars of perianth attachment are not obvious along the peduncle in Paleosecuridaca, the relative length of peduncle and/or gynophore is unclear (fig. 2A, 2F, 2H). In our study of herbarium specimens of several species of Securidaca (e.g., Securidaca longipedunculata Fresen., Securidaca welwitschii Oliv.), we noted considerable variation from one specimen to the next and among different species in relative length of peduncle versus gynophore. Additionally, many of the herbarium sheets and photographs we studied, including those of S. longipedunculata Fresen. and Securidacaatro-violacea Elmer, had mature fruits lacking perianth parts (e.g., fig. 4A), suggesting that the floral remains are early deciduous and that evidence of their attachment may be quite subtle. Crane et al. (1990) were concerned about the lack of perianth parts in the Almont fossils, as they were thought to be typical of modern Securidaca fruits. We suggest that their lack in Paleosecuridaca is not a character useful in delimiting the genus. Additionally, in several blocks we found stringlike structures accompanying the samaras, which might be pieces of the vine to which the fruits would be attached, as in modern Securidaca (fig. 4A).

Fossil Record and Evolution within the Polygalaceae

With the recognition of the anatomically preserved P. curtisii and possibly the compression-impression samara Deviacer (fig. 4B, 4C) as closely related to extant Securidaca, we are now able to expand the fossil record of the family Polygalaceae to include megafossil reproductive remains. Similarities between Paleosecuridaca and the compressed fruit Deviacer are obvious, and it
may be that Deviacer represents an alternative preservational type of the same group of fruits. However, a detailed comparison of these compressed fruits with Paleosecuridaca is beyond the scope of this article. Manchester (1994) provided a description of Deviacer from the Clarno Nut Beds, and we have studied additional specimens from Republic, Washington (fig. 4B, 4C). In general, the compressed samaras of Deviacer are somewhat smaller than Paleosecuridaca. It is interesting that, as in Paleosecuridaca, the wing and nut structure and angles of positioning are quite variable within a given locality, suggesting that taxonomic characters in this group must be evaluated with particular care. It is also intriguing that Deviacer was apparently known from a wide variety of Paleocene and Eocene sites in western North America, Europe, and Asia, suggesting that this plant was widely dispersed in the Paleogene.

Besides these fossil fruits, fossil leaves from the Miocene of Oregon have been attributed to the family (J. A. Wolfe, unpublished data; Collinson et al. 1993). This material is in need of reexamination. Petrified wood for the family has been noted from India (Lakhanpal 1970) and South Africa (Bamford and de Wit 1993).

The fossil record of Polygalaceae is otherwise represented by pollen, and that of Securidaca is highly distinctive and would be easily recognized if present. Occurrences referred to Securidaca are known from the middle Eocene of western North America (Leopold and MacGinitie 1972) and the upper Miocene of Mexico (Graham 1976). Also occurring sporadically throughout the Tertiary is pollen with features characteristic of other genera in Polygalaceae, including four-colporate apertures in which endoapertures may fuse, obscure exine stratification, and a smooth surface. Pollen assignable to the Mommina type is first described from the Paleocene of Chile (Doubinger and Chotin 1975; Muller 1981) as Psilastephano- colporites fissilis. This taxon was originally known from the Eocene of Guyana (Leidelmeyer 1966) and has been considered to be similar to that of extant Mommina (Heusser 1971). Polygalacidites calinus is known from the lower and upper Eocene of Assam, India (Sah and Dutta 1968), cf. Bredemeyera Willd. from the upper Miocene of Mexico (Graham 1976), and Xanthophyllum Roxb. from the upper Miocene of northwestern Borneo (Muller 1981). Taylor (1990) adds to the record with additional reports of pollen from the Eocene of southeastern North America and California (Frederiksen 1980, 1983), and several additional pending and rejected forms have been referenced (Muller 1981).

**Phylogeny and Biogeography**

The presence of fossil taxa assignable to Polygalaceae is significant to researchers reconstructing the phylogeny of the family and deciphering its historical biogeography. Today, the family is distributed throughout the Tropics and subtropics, with one genus, Polygala, having a broad distribution spanning into temperate regions (Miller 1971; Eriksen and Persson 2007). Genera such as Xanthophyllum and Salomonia Lour. are restricted to tropical and subtropical Asia (including Australia), while others are strictly American in present distribution (e.g., Mommina, Moutabea Aublet., and Pteromommina B. Eriksen) or confined to New Caledonia (Balgooy Morat and Meijden) or Australia (Comesperma Labill.). Securidaca occurs throughout the Tropics, from the Americas to Africa and Asia (but not Australia). Although the genus has never been monographed, the majority of the 80 recognized species are found in dry to humid forests in America, with only two...
known from Africa and eight described from southern Asia. Most of the species are climbers (lianas) and rarely shrubs or small trees (Johnson 1987; Eriksen and Persson 2007).

This distributional pattern is one that is not unusual, and disjunctions similar to those found in Polygalaceae have been addressed for other flowering plant families. Recently, several biogeographical studies have used fossil representatives as calibration points for estimating divergence times for clades on well-resolved trees constructed on the basis of molecular data sets in which the genera have been adequately sampled (Malpighiaceae [Davis et al. 2002], Melastomataceae [Renner 2004], and Anisophyllaceae [Zhang et al. 2007]).

At present, the method of choice for reconstructing the biogeographical story of taxa has been the use of dispersal-vicariance analysis (DIVA) to estimate ancestral areas (Ronquist 1997). However, this approach uses only the topology of cladograms on the basis of the extant genera and their current distributions and not the estimated ages of their clades. Distributions of fossil taxa and their use in calibrating molecular phylogenies therefore provide an integral, independent means of testing hypotheses generated by DIVA analyses. In this context, it is important to consider where we stand with regard to the results of recent phylogenetic analyses, as well as the known fossil distributions of Polygalaceae, when considering biogeographical scenarios for the family.

The first molecular phylogenetic study of Polygalaceae was based on sequences of the chloroplast trnL-F region sampled from 73 species within the family, which consists of ~20 genera and 1000 species (Persson 2001). The analysis did not produce the well-resolved tree(s) needed for DIVA analyses. Furthermore, the broad polyphyly of Polygala demonstrated by the analysis indicates the need for that genus to be taxonomically treated to clarify generic boundaries within the family. However, this initial analysis provides valuable evidence for the sister group relationship of Xanthophyllum to the rest of the family, as well as support for the monophyly of Securidaca. Furthermore, the most recent phylogeny for Polygalaceae (Forest et al. 2007), which included expanded sampling of taxa throughout the Fabales using sequences from the trnL-F spacer and intron and one additional region, rbcL, still supports the basalmost branching position of Xanthophyllum within Polygalaceae and the monophyly of Securidaca. We note that only three species of Securidaca were sampled out of the ~80 recognized within the genus.

Extant Xanthophyllum has a distribution centered in Indo-Malesia with some members extending into India, Southeast Asia, and Australia (Stevens 2001). Members of Xanthophylum produce drupes, and multiple dispersal mechanisms (ornithochory, endozoochory, and barachory) are present within the genus (Forest et al. 2007). A DIVA analysis, again based on extant distributions, would strongly suggest an Indo-Malesian center of origin for the family.

To our knowledge, there is no known fossil record of Xanthophyllum. Interestingly, this genus shares a roughly congruent extant distribution in Indo-Malesia with the prominent mangrove palm Nypa Steck. (Baker et al. 1998). The extensive fossil record of Nypa, however, captures a history of much broader occurrence for the genus than its current distribution and includes reports from the Bengal Basin, Borneo, Sarawak, Nigeria, Cameroon, and Venezuela (Ellison et al. 1999). Clearly, in the past, Nypa was a significant member of mangrove communities throughout the world (Gee 2001), and its distribution expanded and contracted in concert with the changing availability of areas with conditions favorable to the mangrove habitat. Nypa thus serves as an example of a plant that has a complex distributional history that today is found only within Indo-Malesia. This is a complex history that cannot be predicted by examining the end point (i.e., the extant distribution) alone. Although a fossil record is still unknown for Xanthophyllum, it could easily have a more restricted distribution, like Nypa, despite being a once widespread taxon.

The lack of a clearly established megafossil record for the Polygalaceae to date has limited our understanding of the family’s evolutionary history. However, it is often the case that once a family is recognized in the fossil record, the likelihood of finding additional representatives from that family increases as critical taxonomic characters are assessed and compared. Indeed, additional studies of fossils potentially assignable to the Polygalaceae from the Paleogene of western North America are currently being completed.

At present, the phylogenetic relationship of Polygalaceae to other members of Fabales (APG 2003) is largely unresolved. Several molecular phylogenetic studies place Polygalaceae as the sister group to the remaining lineages of Fabales (Crayn et al. 1995; Kajita et al. 2001) or Quillaja as sister to the rest of Fabales (Lavin et al. 2005). The most recent and extensive attempt (in terms of sampling for Polygalaceae) to resolve these lineages using Bayesian analyses of molecular sequence data by Forest et al. (2007) shows that although interfamilial relationships within Fabales are not well supported, Leguminosae, Saururaceae, Polygalaceae, and Quillaja (only one of about four species sampled) are all monophyletic with high posterior probabilities (PP = 1.0). Ultimately, the combination of a well-resolved and well-supported phylogeny of Polygalaceae and its position in Fabales, with dated and distinctive megafossils, such as P. curtisi from this family, will permit a more accurate estimate of the age of Polygalaceae and its biogeographic history.

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Literature Cited

APG (Angiosperm Phylogeny Group) II 2003 An update of the Angio-
sperm Phylogeny Group classification for the orders and families of

Augspurger CK 1986 Morphology and dispersal of wind-dispersed

Baker WJ, MJE Coode, J Dransfield, MM Harley, P Hoffmann, RJ Johns 1998 Patterns of distribution of Malesian
Backbuys, Leiden.

Bamford MK, MCJ de Wit 1993 Taxonomic description of fossil
wood from Cainozoic Sak River terraces, near Brandvici, Bushman-

Bluemle JP 1983 Geologic and bedrock map of North Dakota. North
Dakota Geological Survey Miscellaneous Map 25. North Dakota
Geological Survey, Bismarck.

——— 2000 The face of North Dakota. 3rd ed. Educational Series

Brown RW 1962 Paleocene floras of the Rocky Mountains and Great
Survey, Washington, DC.

Burnham RJ 1995 A new species of winged fruit from the Miocene of

Burnham RJ, NL Carranco 2004 Miocene winged fruits of
Tipuana ecuatoriana (Leguminosae). Am J Bot 82:1599–
1607.

Burnham RJ, NL Carranco 2004 Miocene winged fruits of

Collinson ME, MC Boulter, PL Holmes 1993 Magnoliophyta (“An-
giospermae”). Pages 809–841 in MJ Benton, ed. The fossil record.

Corner EJH 1976 The seeds of dicotyledons. Vols 1, 2. Cambridge

Crane PR, SR Manchester, DL Dilcher 1990 A preliminary survey of
fossil leaves and well-preserved reproductive structures from the
Sentinel Butte Formation (Paleocene) near Almont, North Dakota.
Field Geol, NS, 20:1418.

Crayn DM, ES Fernando, PA Gadek, CJ Quinn 1995 A reassessment
of the familial affinity of the Mexican genus Recchia Mocinito and
Sesse ex DC. Brittonia 47:397–402.

Davis CC, CD Bell, S Mathews, MJ Donoghue 2002 Laurasian
migration explains Gondwanan disjunctions: evidence from Mal-

Doubling P, J P Chotin 1975 Etude palynologique de lignites Tertiaires
du bassin d’Arauco-Concepcion (Chile). Rev Esp Micropaleontol 7:
549–565.

Ellison AM, EJ Farnsworth, RE Merkt 1999 Origins of mangrove
ecosystems and the mangrove biodiversity anomaly. Global Ecol
Biogeogr 8:95–115.

Erikson B 1993a Floral anatomy and morphology in the Polygala-

Erikson B 1993b Phylogeny of the Polygalaceae and its taxonomic

Erikson B, C Persson 2007 Polygalaceae. Pages 345–363 in K Kubitski,

Forest E, MW Chase, C Persson, PR Crane, JA Hawkins 2007 The role of biotic and abiotic factors in evolution of ant dispersal in the

Frederiksen NO 1980 Sporomorphs from the Jackson group (Upper
Eocene) and adjacent strata of Mississippi and western Alabama.
US Geol Surv Prof Pap 1084:1–75.

——— 1983 Middle Eocene palynomorphs from San Diego, Cali-
ifornia. 2. Angiosperm pollen and miscellanea. Am Assoc Stratig-


Graham A 1976 Studies in Neotropical paleobotany. II. The Mio-
cene communities of Veracruz, Mexico. Ann Mo Bot Gard 63:
787–842.

Green DS 1980 The terminal velocity and dispersal of spinning sama-

Heusser CJ 1971 Pollen and spores of Chile. University of Arizona
Press, Tucson.

Johnson CT 1987 Taxonomy of the African species of Securidaca

Judd WS, RW Sanders, MJ Donoghue 1994 Angiosperm family

Kajita T, H Ohashi, Y Tateishi, CD Bailey, JJ Doyle 2001 rbcL and
legume phylogeny, with particular reference to Phaseoleae, Mil-

Kihm AJ, JH Hartman 1991 The age of the Sentinel Butte Formation,
North Dakota. J Verteb Paleontol 11:40A.

Kruger H, PJ Robbertse 1988 Floral ontogeny of Securidaca longe-
pedunculata Fresen. (Polygalaceae), including infraspecific mor-
phology. Pages 159–167 in P Leins, SC Tucker, PK Endress, eds.

Kruger HMJ, MJ van der Merwe, PJ Robbertse 1988 Floral organo-
genesis in Securidaca longepedunculata and Polygala virgata var.

Kuhanpal RN 1970 Tertiary floras of India and their bearing on the

Lavin M, PS Herendeen, MF Wojciechowski 2005 Evolutionary rates
analysis of Leguminosae implicates a rapid diversification of

Leidelmeyer P 1966 The Paleocene and Lower Eocene pollen flora of
Guyana. Leids Geol Meded 36:49–70.

Leinfellner W 1972 Zur Morphologie des Gyno ¨ zeums der Polyga-
laceae. Oesterr Bot Z 120:51–76.

Leopold EB, HD MacGinitie 1972 Development and affinities of
Tertiary floras in the Rocky Mountains. Pages 147–200 in A Graham, ed. Floristics and paleofloristics of Asia and eastern North

MacGinitie HD 1953 Fossil plant of the Florissant beds, Colorado.
Institute, Washington, DC.

Manchester SR 1994 Fruits and seeds of the Middle Eocene Nut Beds
flora, Clarno Formation, north central Oregon. Palaeontogr Am 58:
1–205.

——— 2001 Update on the megafossil flora of Florissant, Colorado.
Pages 137–162 in E Evanoff, KM Gregory-Wodzicki, KR Johnson, eds. Fossil flora and stratigraphy of the Florissant Formation,

Mathews R, RC Brooke 1971 Fossil Taxodiaceae and new angios-
perm macrofossils from Quichena, British Columbia. Syesis 4:209–
216.

Matlock GR 1987 Diaspore size shape and fall behavior in wing-

McClain AM, SR Manchester 2001 Dipteronia (Sapindaceae) from
the Tertiary of North America and implications for the phytogeog-

Miller NG 1971 The genera of Polygalaceae in southeastern United

Mirle C, RJ Burnham 1999 Identification of asymmetrically winged

Muller J 1981 Fossil pollen records of extant angiosperms. Bot Rev
47:1–142.
Myers JA 2007 The latest Eocene Badgers Nose flora of the Warner Mountains, northeast California: the “in between” flora. Geological Society of America Cordilleran Section, Bellingham, WA.


Wehr WC 1995 Early Tertiary flowers, fruits and seeds of Washington State and adjacent areas. Wash Geol 23:3–16.

